



Ph.D. Environmental Sciences

XXVI Cycle

**Optimal conservation strategies
in fragmented landscapes: a case study on two
forest rodents, *Muscardinus avellanarius*
and *Myodes glareolus*, in Central Italy**

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1. INTRODUCTION

1.1. The habitat fragmentation concept

Human-induced fragmentation of ecosystems and natural habitats is considered one of the major threats to biodiversity (Davies et al. 2001). Albeit a considerable effort have been invested in research (Fazey et al. 2005), progresses in conservation measures occur too slowly compared to the current rate of extinction of plant and animal species caused by the fragmentation of habitats (Lindenmayer & Fischer 2007). The delay is mainly due to the complexity of the processes involved, which produce a multitude of effects, both direct and indirect, occurring at various spatial scales and levels of biological organization (Lindenmayer & Fischer 2007, Henle et al. 2004). Actually, “habitat fragmentation” is a wide concept reflecting at least four distinct processes:

- **habitat loss**, the progressive reduction of the availability of resources and conditions necessary for presence and persistence of a species (Lindenmayer & Fischer 2007);
- **habitat fragmentation *stricto sensu***, the splitting of a continuous habitat in fragments getting smaller and more isolated from each other (Fahrig 2003, McGarigal & Cushman 2002);

- **connectivity disruption**, the decrease in the permeability of the landscape to individual movements among the fragments (Taylor et al. 1993, Bani *et al.* 2006, Crooks & Sanjayan 2006, Mortelliti *et al.* 2010b, 2011);
- **habitat degradation**, the deterioration of the quality of the habitat (Mortelliti et al. 2010a).

These processes rarely happen with random patterns (Lindenmayer and Fischer 2006). Relicts of original vegetation survive often in areas not suitable to other land uses and not profitable from the economic point of view (poor soils, steep slopes, high altitudes). On the other hand, areas with high natural productivity are typically those that are modified most extensively (Lindenmayer and Fischer 2006). The transformation and management of agricultural landscapes, such as those in which this study was conducted, are recognized among the most serious threats to wild populations worldwide (Foley et al. 2005). Understanding which processes exactly affect populations is crucial to define optimal conservation strategies (Fischer & Lindenmayer 2007), i.e. the conservation actions which maximize the benefits for biodiversity.

Habitat loss and fragmentation *stricto sensu* are two distinct processes, which, however, tend to coexist in nature. The first arises from the removal of a certain amount of habitat, while in the second, a certain amount of habitat is divided in smaller portions, so-called fragments or patches. Figure 1.1 shows the relationship between the two

phenomena. In both squares (representing two real landscapes) the total quantity of habitat is the same; the difference between them lies in the way in which the habitat is distributed. In the left square it is rather continuous and concentrated in a single large fragment; whereas in the right square, the same amount of habitat is fragmented into numerous patches of variable size (Fagiani 2009).

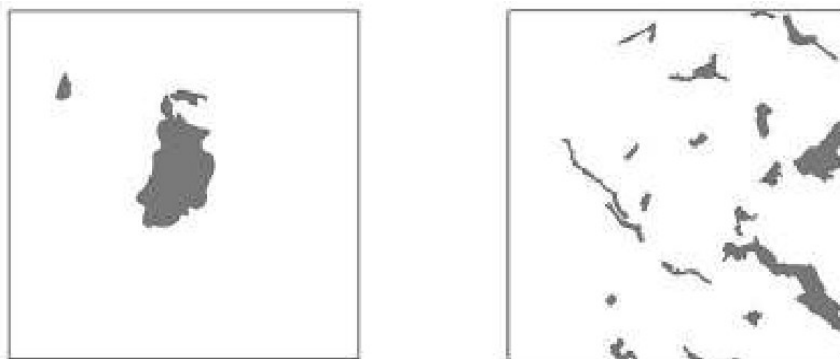


Figure 1.1. Difference between habitat loss and habitat fragmentation *stricto sensu*. The two squares represent two real landscapes with the same amount of habitat (equal level of habitat loss), but different level of habitat fragmentation *stricto sensu* (from Fagiani 2009).

Populations of a given species tend to decline proportionally with

the loss of habitat (Andrén 1994). Below certain levels of remaining habitat, other mechanisms and processes can exacerbate the negative effects of the loss of habitat, accelerating the decline of the populations (Andrén 1994, Liu et al. 2001). Among the main processes of this type there are the habitat fragmentation *stricto sensu* and the habitat degradation.

Fragmentation *stricto sensu* is defined as a process through which a single large portion of the habitat is divided into a number of fragments progressively ever smaller and increasingly isolated from each other by a matrix of habitats different from the original one (Wilcove et al. 1986, Fahrig 2003).

The subdivision of habitat into separated patches leads to the habitat isolation, i.e. the increase in the distances between the fragments which may adversely affect the movements of animals (Lindenmayer & Fischer 2006). Isolation can affect the movement of the animals at different spatial scales and time periods such as daily movements, movements of individuals within a metapopulation, and even movements to a larger scale, as nomadic and seasonal migration movements.

At a local scale, several factors make large fragments more suitable for the persistence of a species compared to smaller fragments. Availability of food, shelter and space (i.e. the habitat quality) can be very limited in small fragments, reducing population sizes (Zanette et al. 2000) and bringing populations closer to the risk of local extinction. Small populations may also be more prone to extinction risks due to

demographic, environmental and genetic stochasticity (Lindenmayer & Fischer 2006).

Negative effects of habitat loss can be detected by either direct measurements of biodiversity, such as species richness (Schmiegelow & Mönkkönen 2002), the abundance and distribution of populations (Hinsley et al. 1995), and the genetic diversity of these populations (Gibbs 2001); or indirectly, by related methods, for example, measuring the rate of growth of a population (Bascompte et al. 2002) or the alteration of species interactions (Taylor & Merriam 1995).

Although studies based on theoretical models (With & King 1999, Urban & Keitt 2001, Fahrig 2002) provide important negative effects caused by fragmentation *stricto sensu* (Fahrig 2003), the results of empirical studies (e.g. Villard et al. 1999, Trzcinski et al. 1999, Yaacobi et al. 2007, Mortelliti et al. 2010b, 2011) have led to conflicting results. These findings suggest that, where detected, the effects of fragmentation *stricto sensu*, are much weaker than those determined by habitat loss, and that, in contrast to theoretical predictions, can be both positive and negative (Fahrig 2003). Such contrasting result might be due to the response level investigated in these researches. The majority of fragmentation studies, in fact, are based on species presence-absence data and the length of the research is often limited to one season of data collection (McGarigal & Cushman 2002; Fahrig 2003; but see Holland & Bennett 2010). These studies are undoubtedly important because they allow detection of fragmentation-related processes involved in shaping species distribution (Fagiani 2009). However, these kind of studies are a

snapshot of reality and do not tell us how the processes affect the demography and dynamics of populations, limiting our ability in planning the optimal conservation measures to enhance the long-term viability of populations in fragmented landscapes. Only studies designed to gather and analyze demographic data collected in the field for more than one season allow determination of population dynamics and viability and detection of processes affecting them.

1.2. The landscape connectivity

Landscape connectivity is the degree of permeability (facilitation or impediment) of landscape elements to movements of individuals among habitat fragments (Taylor et al. 1993). This definition combines the physical structure of a landscape with the response of organisms to that structure. In effect, there are two basic kinds of connectivity: 1) a structural connectivity, i.e. type/kind, quantity, and arrangement of different land uses and structural elements, such as hedgerows, rows of trees, and strips of vegetation and 2) a functional connectivity, that is the types of dispersive movements and capabilities of individuals and species in response to the structure of the landscape. Two fragments of habitat, although not structurally linked, might be connected from a functional point of view. In fact, some organisms, thanks to their dispersive ability, are able to deal with the inter-fragment distances, or cross the matrix, which separates the habitat fragments (Hinsley 2000, Bélisle & Desrochers 2002). Bennett et al. (2004) found a positive correlation between the richness of forest avifauna within fragments of

small size and the presence of tree hedges in the matrix. On the other hand, an element of structural connectivity, for instance, a corridor of riparian vegetation, is not functional when is not used. The distinction between a structural and a functional connectivity, therefore, proved to be of crucial importance in the study of the internal dynamics of a landscape.

Moreover, this is a key consideration today, since many of the previous studies aimed at estimating the landscapes connectivity are based on the analysis of the only structural components and subsequent extrapolation, unsupported by direct data on the actual movements of the species. In fact, when some studies have investigated the relationship between the landscape structure and the dispersive dynamics of a species, the results revealed the existence of peculiar dynamics. For example, if movements occur from one patch to another, it is not evident whether movements in the opposite way would occur, because the latter fragment may have other, closer, fragments, in which the individuals would disperse more easily without ever reaching the first fragment (asymmetric connectivity; Ferreras 2001). The choice of the patch to colonize may be non-random or/and determined by several factors, such as the distance or the quality of the patch or of the matrix, or may be determined by other types of stimuli: e.g., the cactus bug (*Chelinidea vittiger*) locates its habitat with the sense of smell so the choice is determined by the direction of the wind (directional connectivity; Schooley & Wiens 2003). Van Langevelde (2000) found that in some bird species, a fragment is chosen with greater chance if it is already

occupied by conspecifics. These examples serve to illustrate why the connectivity of a landscape cannot be captured by indices that take into consideration only the structural elements (Taylor et al. 2006).

To achieve a single definition of connectivity that embraces the many nuances of this complex phenomenon and that is verifiable in any environment and at any time is, to date, considered to be an untenable goal. The crucial difficulty resides mainly in the characteristics of the phenomenon: connectivity is a process/pattern entirely target and scale dependent. Definitions (Taylor et al. 2006), metrics of analysis (Bender et al. 2003), conservation applications (Bennett 1999) and extent of their success depend on the investigated taxa, the spatial and temporal scales under consideration, as well as the territorial context. This obviously does not mean that it is necessary to know all the measures of connectivity for each combination of species and landscape mosaic. Rather, recognizing wide variability of responses to an equally high variability of structures, we must determine the ranges that include intervals of responses that embrace the widest ranges of taxa and spatial scales (Taylor et al. 2006). Clear, feasible and replicable metrics of landscape connectivity are vital in a context of limited time and resources (Calabrese & Fagan 2006).

1.3. Habitat quality

Habitat degradation is the process that leads to a gradual deterioration of the quality of habitat. It can occur regardless of habitat loss and fragmentation, although it may be facilitated and exacerbated

by these two processes (Mortelliti et al. 2010a). Most studies have focused on habitat loss and fragmentation *stricto sensu*, while the role of habitat quality in fragmented landscapes has been overlooked, especially because of the difficulties in the choice of its quantitative measures (Mortelliti et al., 2010a). However, there are several studies that highlight its role in determining the distribution patterns of species (Thomas et al. 2001; Holland & Bennett 2007; Mortelliti & Boitani 2008), the abundance of the populations (Lloyd 2008), and the dynamics of colonization and extinction (Franken and Hik 2004).

The habitat quality has been defined as the ability of the environment to provide conditions for the persistence of individuals and populations (Hall et al. 1997). Van Horne (1983), however, has defined the quality of the habitat as the average of individual fitness (in terms of density, fecundity and survival) per unit of surface. Pulliam (1988), in his work on the structure of the source-sink populations, interpreted habitat quality based on the source/sink dynamics: the births in the "source high-quality habitat" exceed the deaths, while emigration rate exceeds the immigration rate. On the opposite, in the "sink low-quality habitat" the deaths overcome the births, and the immigration rate exceeds the rate of emigration.

While habitat quality is often seen as a major cause of the source-sink dynamics (Thomas & Kunin 1999), these could be the result of several other factors (Kaweki 2004). In fragmented landscapes, for example, the geometric properties of the fragments have different effects on animal populations, including the influence on demographic

parameters such as survival and emigration rates (Hanski and Gaggiotti 2004). Indeed, in this case, several factors such as: a) the spatial structure which surrounds the focal fragment, b) the characteristics of the matrix, c) the perceptual range and the dispersal ability of individuals, which determine the possibility of reaching another fragment (Schooley and Wiens 2003), play an important role. These characteristics can be quantified with a function of dispersion (Wiens 2001), but are not related to habitat quality. At the same time, even if there is no empirical evidence, it cannot be excluded that the fragments of high quality produce healthy individuals who can complete the dispersion with greater success. In other words, it can be quite complicated to distinguish the role of the habitat quality as that of the spatial configuration (Pöyry et al. 2009, Zheng et al. 2009).

1.4. Habitat fragmentation studies at the population level

Most fragmentation studies are focused on the distribution of species, making inference from analysis of presence/absence data. Although these studies might allow the prediction of the species distribution patterns, they do not allow to explain why and how the populations goes extinct in fragmented landscapes, as well as not grasping the ultimate causes of extinction.

There is a substantial difference between explaining a process and predicting the probability that a certain event occurs. An explanation of the distribution of species in fragmented landscapes requires an understanding of the relationship between causes and effects of the

distribution pattern observed (Mortelliti 2013). Still few studies have collected the information that really allows making inference about the processes that determine the distribution pattern of the species (Mortelliti et al. 2010c).

Since conservation biology is a science of crisis, there has always been a strong attention to the predictions rather than towards the explanations of a phenomenon (Soulé 1986). Predictions are often made with the habitat suitability models. These models allow with sufficient precision to predict the distribution of a species as a function of certain predictive variables (for example the size of a fragment), but the demographic processes that determine how species respond to fragmentation are poorly understood (Holland & Bennett 2010). That means that we are not actually explaining the distribution, that is, the causal link between the size of the patch and the presence of the species (Mortelliti et al. 2010c) .

There is growing empirical evidence showing that the fragmentation impacts on demographic parameters. Holland & Bennett (2010), for example, have shown that the size of the patch influences many aspects of the demography of the populations of *Rattus fuscipes*, such as density, age structure and immigration rate. Hanski & Gaggiotti (2004) have shown that in fragmented landscapes the geometrical properties of patches alter the main demographic parameters of a population, such as survival and migration rates. Therefore, it is a top priority to broaden the field of investigation in the research on the distribution of species susceptible to the processes of habitat

fragmentation and loss, by analyzing demographic parameters of paramount importance, but rarely considered, such as population abundance, survival, sex ratio, fertility, dispersive behavior. In this way we will bridge the gap between the ultimate cause (e.g. small patch size) and its effect on populations (e.g. population extinction), which is what hinders a clear explanation of patterns of presence (Mortelliti 2013). Studying demographic parameters means understanding, for example, that the local extinction in a patch is carried out for an asymmetric sex ratio which resulted in a small recruitment rate of the local population, leading ultimately to extinction.

Previous studies on the dormouse in fragmented landscapes of central Italy, using presence/absence data, have shown that the greatest threat to the species is the loss of habitat, while the role of fragmentation *stricto sensu* is smaller (Mortelliti et al. 2011). But studies that rely solely on data of presence/absence, as we have seen, should be interpreted with caution since they could mask critical processes that occur at the population level (Holland & Bennett 2010). Hence the need to repeat the study distinguishing the effects of loss of and habitat fragmentation *stricto sensu* at the demographic level. In the common interest to improve the management interventions and conservation , both in terms of effectiveness and cost, it is important to understand how species react to the process of fragmentation. These findings might have a wider impact on the long-term conservation of species in fragmented landscapes compared to occupancy models (Mortelliti et al. 2010c).

1.5. Spatially structured populations

In fragmented landscapes, many species are spatially structured, composing a set of discrete populations within each habitat fragment that interacts with each other. There are several possible dynamics that spatially structured populations might present. Harrison (1991) proposed a classification with four main types (Fig. 1.2):

- classical metapopulation, composed by a set of conspecific populations that persist in dynamic balance between extinctions and colonization in each fragment (Levin 1970);
- source-sink populations, a set of subpopulations, some of which experience local extinctions (sink populations) but the persistence of the regional population is not affected because maintained by migration from other populations (source populations; Hanski & Gilpin 1991, Pulliam 1988, 1996);
- patchy populations, a set of populations where the high rates of dispersal hold these populations together in what could be considered a single demographic entity. The probability of extinction of local populations is very low and therefore they can not be considered as a metapopulation (Bascompte et al. 2002);
- non-equilibrium metapopulation, typical of highly fragmented environments where extinction is not offset by recolonizations (Hanski 1998; Bolger et al. 1997).

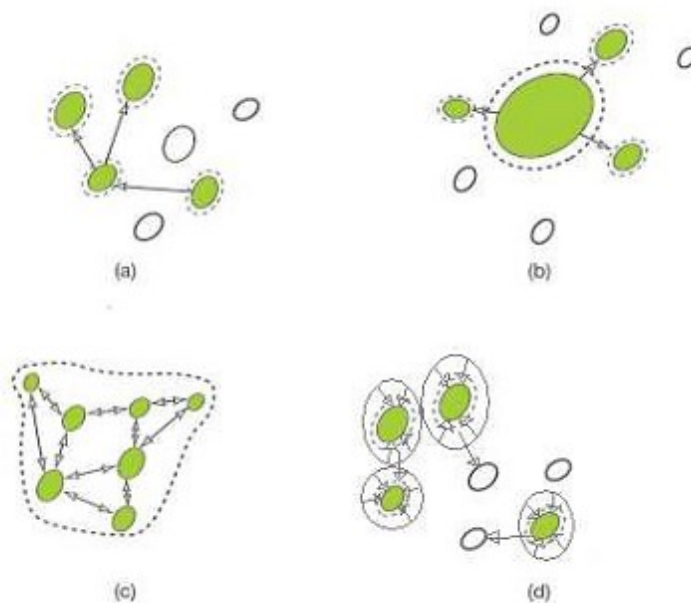


Figure 1.2. Different types of spatially structured populations. a) Classic metapopulation. b) Source-sink populations. c) Patchy populations. d) Non-equilibrium population. While in a, b and c the arrows represent only the movements of individuals among the fragments, in d they point out also a decrease in population size due to a regional decline (see text for a definition of non-equilibrium populations; figure from Harrison 1991).

Some authors are in disagreement with the use of these categories since the natural world does not have clear boundaries between one type

and the other (Hanski & Gaggiotti 2004). Within an area, for example, the same species may present simultaneously population dynamics that falls into more than one of these categories. On the other hand in ecology has increasingly recognized the importance of non-equilibrium dynamics of natural populations, which are characterized by frequent local extinctions and recolonizations (Akçakaya 2002). In this case, although each local population may exist for only a short period of time, the entire population can persist for a long period.

The risk of extinction of a local population is determined by factors such as population size, demographic and environmental stochasticity. However, the risk of extinction of a spatially structured population depends also on other factors that operate at the level of the metapopulation. These include the number and spatial configuration of habitat patches that are occupied by local populations, the similarity of environmental conditions in the different fragments, and the migrations between the populations that may lead to the recolonization of empty patches (Akçakaya 2002).

Many researchers erroneously identify several spatially structured populations as classical metapopulation. However, a metapopulation could be classified as classical only if: i) habitat is distributed in discrete patches, ii) dynamics of the local population are not synchronized and there is evidence of processes of local extinction and colonization, and iii) there is no evidence of dispersion among the local populations (Hanski 1999). Most of the studies on mammals used the dispersion as experimental evidence of the presence of a metapopulation. Although it

is undeniable the importance of its role, dispersion by itself can not be considered a reliable indicator, but it should be combined with other requirements.

Therefore, the use of the concept of metapopulation is not always supported by empirical evidence, especially in mammals. In this regard, Oliver et al. (2009) showed that only five populations of mammals in the world presented the requirements of the classical metapopulation concept.

1.6. Spatially explicit population models (SEPMs)

Spatially explicit population models (SEPMs) are an important tool to study the dynamics of spatially structured populations, allowing to perform spatially explicit population viability analysis (PVA) of metapopulations. The composition of the landscape, the spatial arrangement and vegetation characteristics of the fragments play a vital role in determining the dynamics of spatially structured populations in fragmented landscapes (Fahrig & Merriam 1994; Wiegand et al. 1999). As an example, the distances between two fragments affect the dispersion rates, an important parameter in determining the risk of extinction of a species (Akçakaya et al. 1999; Root 2004). Through SEPMs, metapopulation models run on a map of the real landscape. This map allows to explicitly incorporate: the positions and demography of the populations; the fragment characteristics or other elements of interest (such as corridors, vegetation characteristics).

SEPMs require spatial data, arising from map layers built with

GIS softwares, where the ecological requirements of the species are georeferenced. Attributes can be assigned to the fragments randomly or with a specific pattern (Lamberson et al. 1994; Dunning et al. 1995). This is done by assigning habitat characteristics, relevant for the species, in each cell of the grid (Murphy & Noon 1992; Noon & McKelvey 1992). The input of these data could be done through the use of land use maps, vegetation cover maps or by any other map that contains the characteristics of some aspect of habitat important for the species (e.g. temperature, precipitations, etc.). Through the setting of a habitat suitability function, SEPMS construct an habitat suitability map where the habitat fragments which can support the individual populations are identified. The spatial structure of the habitat fragments is then combined with demographic parameters (such as carrying capacity, fertility rate, survival rate, etc.) of the species under investigation and with data on its dispersive behavior and mechanisms (Akçakaya 1996). The performing of the SEPMS then allows the assessment of the species extinction risk, making possible also to explore different management options (Fig. 1.3).

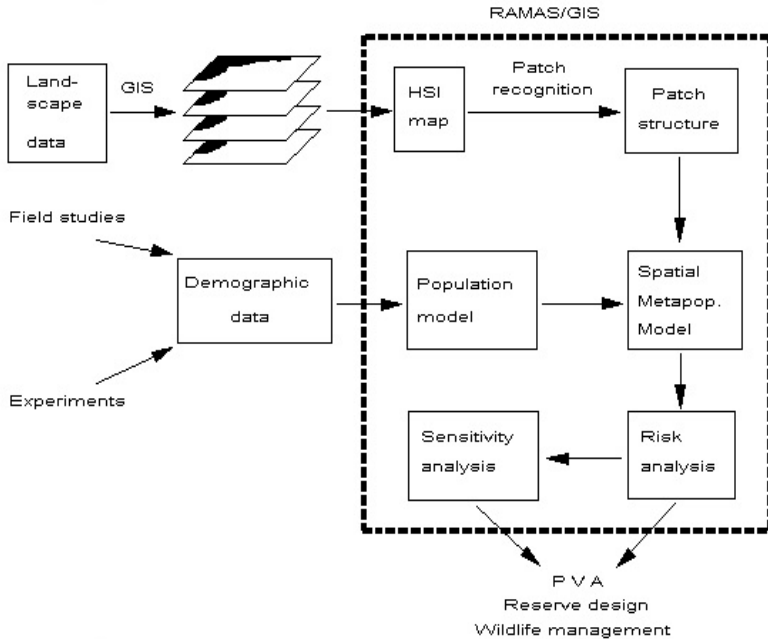


Figure 1.3. Conceptual framework of the SEPMs (from Akçakaya 2002).

It was shown how the dispersive ability of a species can determine the way a population successfully exploits a given landscape, constituting the limiting factor in determining the future size of the population that can be sustained in the landscape (Root 2004). The mortality rate during among-fragments movements might depend on many factors, such as: the dispersive ability of the species, the type of

motility, the distances among the populations, the habitat type used during dispersion (Akçakaya 2004). It is therefore of paramount importance that dispersion could be modeled in the analysis of metapopulation persistence. A key feature of SEPMs is that they may incorporate the displacements of individuals between the different patches of the landscape and are able to analyze how these movements affect the dynamics of the spatially structured populations (Dunning et al. 1995).

However, parameterization of the dispersion process is particularly challenging since, in general, we have a scarce knowledge on how the species perceive the various landscape elements. Ecologists willing to make quantitative predictions with the SEPM, should recognize the need to invest considerable effort in the field gathering of as more as possible data on inter-fragment movements of the species.

Two main types of spatially explicit population models were recognized: individual-based models and population-based models. In the individual-based models the future position of each individual in the landscape is predicted and the individual acquires the characteristics of fitness associated with the type of cell that it occupies (Lima & Zollner 1996; Wiegand et al. 1999). It is possible to investigate, for example, the individual foraging, growth and predation and all these individual characteristics are ultimately translated into the individual fitness (Turner et al. 1993). The parameters relating to the entire population are then calculated following the fate of all individuals over time. In the population-based models the demographic data are specified for each

population. For abundant organisms, such as rodents or insects, this appears to be the most appropriate modeling approach, since the difficulties to follow the fate of all the individuals of a large population and the excessive computational effort required (Hassel et al. 1991; Palmer 1992).

1.6.1. Usefulness of spatially explicit population models

SEPMs allow to simulate the dynamics of spatially structured populations and predict future distribution and abundance in a given time interval (Boyce 1992, Lacy 1993, Burgman et al. 1993). It is thus possible to evaluate the threats experienced by the different species in terms of risk of extinction or near-extinction, or future decline of a population, as well as several options for their recovery (Ludwig 1999, Brook et al. 1997, 2000; Akçakaya & Sjögren–Gulve 2000) .

The plasticity of the modeling of spatially explicit populations allows the detection of population responses in relation to changes in the amount, arrangement and quality of the habitat (Stevens & Baguette 2008; Baguette & Schtickzelle 2006; Root 1998, Nielsen et al. 2006). It might also predict the potential effects on population viability of the variation in several factors such as the proportion of suitable habitat within the landscape, the size and shape of the fragments or their mutual distances.

In synthesis, the modeling process of SEPMs allows to select particular aspects of a real system and to determine mathematical relationships between these aspects in order to: acquiring the knowledge

on how the system works; predicting its evolution in the future; making decisions about how to manage it (Akçakaya 2005).

Although SEPMs could not completely replace the field studies, they allow overcoming the limits of space and time scales imposed by the logistical difficulties of field research (Dunning et al. 1995). It is in fact impossible to design field experiments in which you can control and manipulate each environmental parameter, especially for those processes that operate on large scales (Turner et al. 1989a , b; Johnson et al. 1992). The replication of the experiments on a large scale is sometimes excessively expensive and it is often difficult to obtain a statistically significant sample size. The simulations of a model, however, may be replicated several times in order to obtain an estimate of the range of potential effects (Turner et al. 1995).

In the present research, the field study was aimed to collecting data and estimating the demographic parameters to be used to parameterize the SEPMs. For a relatively small spatial scale, we believe that the integration of the field and modelling approaches might i) better explain the complex processes involved in the population dynamics of the species under investigation, and ii) allow the identification of the optimal conservation strategies for the species in fragmented landscapes.

Usefulness of SEPM is not limited only to study the fragmentation effects, but encompasses many other fields. It is recognized particularly useful, for example, in the study of complex interactions in a predator-prey system (Griffin & Mills 2004) and the transient behavior of a population (Lamberson et al. 1992). Other fields

of application include the wildlife management, such as the planning of programs of introduction, reintroduction and translocation (Schadt et al. 2002, Mladenoff et al. 1999), the predator control (Akçakaya 2004, Griffin & Mills 2004), the spread of invasive species (Rushton et al. 1997), the analysis of the effects of hunting pressure (Sezen et al. 2004), and the planning of timber harvest (Griffin & Mills 2004, Liu et al. 1995).

Communication between land administrators and ecologists remains one of the major challenges; spatially explicit population models provide a common language between these different figures (Burgman et al. 1993, Akçakaya et al. 1999, Sjögren-Gulve & Ebenhard 2000, Beissinger & McCullough 2002, Morris & Doak 2002).

The results of the models can be used to evaluate and analyze the success of different management options, such as habitat restoration or the increase in connectivity, allowing to choose which management strategy can maximize the probability of persistence of a population (Peres 1999; Lindenmayer et al. 1995, Sezen et al. 2004, Gerber 2004, Yamada et al. 2004). It allows developing relative rankings of the different management options (McKelvey et al. 1992) and alternative management strategies can be evaluated and ranked in terms of the viability of the species. The SEPMS are, therefore, of critical importance to provide land managers with optimal conservation measures for different species in a relatively short time.

1.6.2. Limits of the use of SEPM

The initial enthusiasm on the use of SEPMs was dampened by criticisms highlighting the limits of this tool (Doak & Mills 1994; Wennergren et al. 1995; Meir & Kareiva 1997; Ruckelshaus et al. 1997; Beissinger & Westphal 1998; Hartway et al. 1998), particularly on their predictive accuracies (Brook et al. 2000; Fieberg & Ellner 2000, Boyce 1992; Lacy 1993).

Accuracy of predictions of these models is based mainly on the quality of data used to parameterize them. Data collection is often expensive and require demanding field studies to estimate all necessary parameters. The lack of adequate data may limit the useful application of these tools (Doak & Mills 1994; Beissinger and Westphal 1998; Wiegand et al. 2004). However, through sensitivity analysis is possible to examine the relative importance of the parameters that most affect the result and use them to concentrate efforts on the field, in order to improve the estimates of these parameters (Dunning et al. 1995).

Another problem arise from the amplification of uncertainty due to errors during the parameter estimates. A small error in parameter estimates, in fact, might be amplified through a concatenation of calculations, thus affecting the results of the model (Kareiva et al. 1997; Beissinger & Westphal 1998). Ruckelshaus et al. (1997) showed how errors due to uncertainty in the estimate of the mortality in sink fragments, propagated in large errors on success of dispersal of the organisms predicted by the model. As a consequence, one crucial aspect is to understand the way in which the uncertainty of parameter estimates

is propagated. A way to limit the effects of uncertainty is to estimate the confidence intervals (lower and upper limits) of the model parameters (Akçakaya 2004; Lopez 2004).

The results of the models and the data collected in the field on population dynamics do not always coincide (McCarthy et al. 2001a). Such discrepancies are due mainly to the fact that the models are, by definition, imperfect representations of the reality, in addition to the issues abovementioned regarding the uncertainty on data measurement. The purpose of the model validation is to discover major discrepancies, and this is an important part of the use of population models in the management activity (McCarthy et al. 2001b). Validations, however, have rarely been undertaken, especially due to the excessive computational effort (Higgins et al. 2000, McCarthy et al. 2000; Rushton et al. 2000, Wiegand et al. 2004).

1.7. Rodents as model species in fragmentation studies

The effects of loss, fragmentation, isolation and degradation of forest habitats, seem to depend on the level of specialization of the species concerned. As an example, among small mammals, the responses of the bank vole *Myodes glareolus* showed to be almost opposite to those of generalist species such as those belonging to the genus *Apodemus* (Diaz et al. 1999).

The choice of small mammals in fragmentation studies is mainly due to the fact that: a) small mammals showed to have an intense response to the effects of fragmentation both at the landscape and

fragment scale (Bolger et al. 1997, Bright et al. 2006; Morris 2003; Bright & Morris 1996, Juškaitis 2008, Mortelliti et al. 2011); b) the techniques of field research and the extensive bibliography devoted to the basic biology of these species make it particularly easy to gather data on their main demographic parameters (Seber 1973, Krebs 1999, Bright et al. 2006, Juškaitis 2008).

Two rodents were selected as target species in the present research: one arboreal, the hazel dormouse *Muscardinus avellanarius*, and one terrestrial, the bank vole *Myodes glareolus*. The differences in the biology of these species (e.g. different habitat requirements for feeding, breeding and shelter against predators) suggest different responses to the habitat fragmentation processes and, consequently, different responses to different land management and/or conservation strategies.

Arboreal rodents: *Muscardinus avellanarius*

Arboreal mammals, such as arboreal marsupials, tree squirrels and dormice are often threatened by habitat loss and fragmentation (Lindenmayer et al. 1999, Koprowski 2005). In European regions, various single-species studies have been carried out, suggesting similar responses in this guild of mammals (e.g. see Bright et al. 1994 on the common dormouse, Rodriguez and Andr en 1996 on the red squirrel, Capizzi et al. 2003 on the fat dormouse).

The strong specialization of the hazel dormouse *Muscardinus avellanarius*, a strictly arboreal rodent, to forest environments

determines its vulnerability to the processes of habitat loss and fragmentation (Andrén 1997a, b; Delin & Andrén 1999). The maturity of the wood, the size and the internal structure of the patch, and the degree of isolation influence the distribution of this species (Bright et al. 1994, Mortelliti et al. 2009a). Moreover, the hazel dormouse tends to avoid movements on the ground (Bright 1998). In Great Britain the processes of habitat loss and fragmentation are the major threat of the species extinction (Bright & Morris 1996).

The perception of the landscape by a strictly arboreal species, such as the hazel dormouse, with a net distinction between landscape elements (patches, corridors and matrix), make it a good model species for studies on fragmentation effects.

Terrestrial rodents: *Myodes glareolus*

It was determined that the fragmentation-related processes cause changes in the structures of rodents community, with a reduction of the diversity and an increase of generalist species (Millán et al. 2003; Mitchel et al. 2006).

The bank vole *Myodes glareolus* is considered a specialist species of forest habitats with limited dispersive capacity (Geuse et al. 1985, Van Apeldoorn et al. 1992, Kozakiewicz et al. 1999) and, for this reason, it is considered a good model species for studies on the effects of fragmentation.

Various studies have focused on terrestrial rodents in fragmented landscapes (Bolger et al. 1997, Van Apeldoorn et al. 1992), and both

configuration of habitat patches and patch quality are suspected to shape the distribution of these species.

Van Apeldoorn et al. (1992) and Paillat and Butet (1996) have hypothesised that terrestrial rodents populations (specifically the bank vole *Myodes glareolus*) in fragmented landscapes will be structured as metapopulations. However their studies were based on the doubtful assumption that if a species was not caught within 48 hours it could be considered absent (or extinct if captured previously) and no attempt was made to fit metapopulation models to their data. Therefore, the conclusions reached by these authors can be been misleading by not having considered that, in some cases, the extinctions may have been confused with a decrease in the probability of capture (Mortelliti & Boitani, 2007). Despite this, bank voles are able to survive in small patches in highly modified landscapes, with limited remaining forest cover (Millán 2003, Mortelliti et al. 2009b). It appears most likely a type of dynamic patchy population, as suggested by Szacki (1999) and Mortelliti et al. (2010).

1.8. The conservation of biodiversity in fragmented landscapes

The loss and fragmentation of habitat are actually very widespread at every spatial scale, and the establishment of protected areas alone cannot ensure the long term and large scale conservation of many species, communities and ecosystems (Margules & Pressey 2000). There is an urgent need to find quickly conservation strategies that enable to maintain the vitality of the species and the functionality of

ecosystems outside of protected areas, i.e. in areas subject to transformation and disturbance (Pullin 2002).

The development of strategies for the creation of ecological networks (at local, regional and continental scales) is today a worldwide challenge in conservation planning (Boitani et al. 2002, Bani et al. 2002, Soulé et al. 2006, but see for a critique Boitani et al. 2007). By increasing the flow of bodies or the continuity of ecological processes between the different parts of the landscape mosaic, there is the potential to build networks of habitat that integrate the conservation efforts at a multiplicity of levels, including local, regional, continental and even global scales.

Recently, Lindenmayer & Fischer (2006) and Lindenmayer et al. (2007) have argued the importance of a holistic conservation approach through ecosystem management, based on the complementary use of pattern oriented and species/process oriented approaches. Conservation strategies in cultural landscapes based on the first approach include: i) the maintenance of native vegetation (i.e. **habitat preservation**; Moilanen & Wintle 2006, Moilanen 2008, Van Teeffelen et al. 2006, Burgman et al. 2008, Hodgson et al. 2011), ii) the creation of new habitat fragments or the enlargement of small fragments yet present (i.e. **habitat restoration**; Bennett et al. 2000, Noss et al. 2006, Munro et al. 2007, Cunningham et al. 2008, Nicol & Possingham 2010), iii) the creation or maintenance of buffers around focal areas, corridors and stepping stones (i.e. **preservation and creation of landscape connectivity**; Van Teeffelen et al. 2006, Thomson et al. 2009, Visconti

& Elkin 2009, Taylor & Goldingay 2011, Eden & Cottee-Jones 2013), iv) the management of specific attributes of the fragment that often determine local conditions habitat (i.e. **habitat quality improvement**; Bennett et al. 2000, Gomez-Aparicio et al. 2004, Thomson et al. 2009, Visconti & Elkin 2009, Chauvenet et al. 2010). Specific habitat elements, such as those used as shelter, food or breeding resources, are the essential habitat components for the persistence of the species, but they are hardly measurable to a spatial scale or comparable with that of the mosaic (Mortelliti & Boitani 2008, Paquet et al. 2006). On the other hand, the species/processes oriented strategies rely on the maintenance of the interactions (e.g. predation, competition) of key species, the management and control of appropriate disturbance regimes, the control of invasive species and the persistence of endangered species.

1.9. Optimal conservation strategies

Current rates of biodiversity loss are unprecedented in the history of the Earth (Pimm et al. 1995). In response to the accelerating extinction of species, international conservation organizations have generated global biodiversity conservation templates (Brooks et al. 2006) as strategic guidelines to conservation investment. High-profile global scale priority templates include Hotspots (Myers et al. 2000), the Global 200 (Olson & Dinerstein 1998), Endemic Bird Areas (Stattersfield et al. 1998), and Crisis Ecoregions (Hoekstra et al. 2005).

Recently, it has emerged how conservationists would not only need face and find answers to ecological problems, but their analysis

would have to take into account also socioeconomic factors (Montgomery et al. 1999, McBride et al. 2007, McCarthy et al. 2008, Polasky 2008, Polasky & Segerson 2009), since the latter could threaten the success of conservation actions and determine a waste of limited financial resources (Bottrill et al. 2008, 2009). In a world with limited conservation funds (James et al. 1999), and with a great geographical variability in the conservation costs (Balmford et al. 2003, Drechsler 2010), efficiency would be better measured in terms of conservation return on financial investment. It is increasingly recognized that including the economic costs of conservation, to maximize the greatest return on investments (Murdoch et al. 2007, 2010; Underwood et al. 2008), can lead to substantially larger biological gains (Naidoo et al. 2006).

A plethora of optimization procedures were developed to deal with the most important issues in conservation biology: reserve selection (Newburn et al. 2005, Cabeza & Moilanen 2006, Strange et al. 2006, Van Teeffelen & Moilanen 2008, Whitey et al. 2012), habitat restoration (Vesk & Mac Nally 2006, Dorrough et al. 2008, Van Teeffelen & Moilanen 2008, Johst et al. 2011), landscape connectivity (Girvetz et al. 2008, Johst et al. 2011, Gaaff & Reinhard 2012), evaluation of multiple management strategies (Holzkamper & Seppelt 2007, Van Teeffelen et al. 2008), control of pest and invasive species (Choquenot & Hone 2000, Donlan & Wilcox 2007, Baxter et al. 2008, Capizzi et al. 2010), forest management for timber production (Hof & Joyce 1992, Calkin et al. 2002, Ananda & Herat 2009), priority of threatened regions and

species (Ando et al. 1998, Frazee et al. 2003, Bode et al. 2008, Carwardine et al. 2008, Joseph et al. 2008), evaluation of the conservation returns of governmental policies and incentives programs (Wätzold & Schwerdtner 2005, Ohl et al. 2008, Uthes et al. 2010, Armsworth et al. 2012), land use changes (Newburn et al. 2005, Mouysset et al. 2011, Polasky et al. 2011), monitoring programs (Field et al. 2005).

Making decisions about allocation of resources between alternative conservation actions requires a systematic approach (Possingham et al. 2001). The probable outcomes and decisions between them are dependent upon an interaction between the ecological and economic systems, thus requiring a coupled economic and ecological model. Ecological uncertainties resulting from spatial and temporal variation in environmental factors will flow through to economic consequences (Dorrrough et al. 2008).

There is a mismatch between the scale of on-the-ground decisions and the scale at which biological data are available. This mismatch presents severe impediments to the definition of effective conservation, especially in developing countries. Land-use and land-management decisions are made at relatively small spatial scales, and it is the total sum of such local fine-scale decisions across broad landscapes that determines conservation outcomes (Murdoch et al. 2010).

An accurate estimation of the total cost of a policy is required to compare its costs and benefits. Even when the monetary assessment of conservation benefits is difficult, the marginal and total costs of

conservation can still help making informed management decisions (Barraquand & Martinet 2011).

Allocation of conservation resources, like any decision theory problem, requires a broad goal, a specific objective, a set of constraints, a set of possible actions that form a strategy, and an understanding of the system dynamics provided by equations that link the actions and constraints to the objective (Wilson et al. 2006). Responsible conservation organizations and international agencies should consider embracing a theoretic decision approach when scheduling the allocation of conservation resources.

An important part of the budget of the European Common Agricultural Policy has been allocated to schemes that aim at mitigating the environmental effects of agricultural intensification (Otte et al. 2007), however, their effectiveness in reducing biodiversity loss in agro-ecosystems has been moderate at the best (Kleijn et al. 2001, 2006). To be consistent with the biological scale of population dynamics, the effectiveness of such conservation schemes should be evaluated at the landscape scale (Wu et al. 2004). An important conflict in conservation decisions in agricultural landscapes is that agriculture is the primary and ongoing land user responsible for the generation of income, and conservation benefits are achievable only within this production context (Mouysset et al. 2011).

1.10. Scope, aims and hypotheses of the research

The **scope** of this study is to determine the optimal conservation

strategies in fragmented landscapes for the investigated species. Optimization will be undertaken in terms of maximizing the persistence of populations in a time frame of 50 years at a fixed budget, 1 million of euros, for the implementation of conservation actions.

Aims

- Analyses of demographic parameters of the target species.
- Efficacy and cost-effectiveness evaluation of conservation actions.

Hypotheses and predictions

The main hypotheses driving this research are the following.

M. avellanarius

- As a consequence of the strictly arboreal habit of the species, we predict that *M. avellanarius* populations will be affected by the quantity of the remaining forested habitat, in terms of fragment size (e.g. in relatively small fragments populations might not be viable because of processes affecting small populations, as. inbreeding depression or genetic drift).
- We predict, consistently with recent findings (Mortelliti *et al.* 2011) and as a consequence of its high degree of habitat specialization, that the population dynamics among fragments might be influenced by the interaction of fragment size and the structural connectivity surrounding it. In particular, we hypothesize that fragment size might

interact with the presence and number of connecting structures departing from the fragment. For example, a relatively small fragment might host a small, but persistent, population if the patch is connected by one or more hedgerows which permit the immigration of individuals from other fragments. This might have significant effects on the reduction of extinction probabilities both at the fragment (or local) and metapopulation (or regional) scale.

- An important habitat requirement of the species is a dense shrub layer, diverse in plant species, producing fruits. This habitat specialization is crucial in providing shelter from predation, as well as nesting and food resources. In a forest ecosystem, one of the main factors shaping the structure of the shrub layer is the age of the woodland. Since in our study area forest fragments are mostly managed for timber production, but not all at the same time, they present different maturity stages. Therefore, we expect that in fragments recently managed, and presenting dense shrub layers, survival rates and fertility of the populations will be higher than those in more mature stands.

Myodes glareolus

- As abovementioned, *M. glareolus* are strongly associated with forest habitat. Consistently with recent findings (Mortelliti *et al.* 2009a), we expect that some demographic

parameters (e.g. the sex ratio, the survival rate) of the species would be negatively influenced by decreasing fragment size.

- Terrestrial rodent species are strongly dependent on the availability of their main food resource, acorns. Moreover their distribution and survival seems to be affected by the presence of a well-structured shrub layer (Fagiani et al. submitted). Therefore we expect that acorn abundance and the structure of the shrub layer influence the vital rates (survival and fertility) of *M. glareolus* populations.
- In fragmented landscapes, *M. glareolus* inhabit relatively isolated patches (Mortelliti *et al.* 2009a). We predict that metapopulation dynamics and extinction risks of the species would not be determined by the inter-patch distances and spatial arrangement of the fragments. However, we also hypothesize a potential positive role played by the presence of linear structures (e.g. hedgerows) between fragments which enhance landscape connectivity.

1.11. Outline of the dissertation

In the present research I will determine the main demographic parameters and explore which environmental factors affect the species vital rates, I will project the species viability in the investigated landscapes and I will look for the species optimal conservation strategies in fragmented landscapes. In the scenario of a fixed-budget decision-

making process to determine the optimal conservation strategies (as that of the present research), the determination of which conservation actions would guarantee the persistence of the species in the landscapes mainly depends: 1) on the viability trend, determined for example by a PVA, and 2) on which environmental factors resulted to be the most important in affecting the vital rates and the dispersal dynamics. The temporal trend in abundance and/or occupancy patterns of the spatially structured population of the species, the demographic parameters and the habitat fragmentation-related patterns, will lead the elaboration of the optimization procedure. As an example, if the spatially structured population of the species show a negative temporal trend in abundance and/or occupancy patterns, and if the habitat fragmentation-related patterns more involved in shaping this trend is the fragment size (e.g. by affecting both survival and fertility), then the optimization protocols would be developed in a habitat restoration perspective.

As a consequence, in my work I was able to develop the simulation protocols for the procedure optimization only after I carried out the demographic analysis and the spatially explicit PVA on the real landscape. Therefore, after this first introduction chapter where I presented the background of the study, the investigated species the scopes, aims and leading predictions of my research (**Chapter 1**), I divided the methodological and statistical issues in two sections. In the first section I will expose the field data gathering and the demographic analysis (**Chapter 2**), while in the second section I will present the SEPMS parameterizations and the optimal conservation simulation

protocols, and show the results obtained by applying them (**Chapter 3**).

In a final chapter I will discuss the methodological aspects of the research, the results of the demographic analysis and of the optimization process, and the implications for the conservation of rodents in fragmented landscapes (**Chapter 4**).

2. EFFECTS OF HABITAT FRAGMENTATION ON VITAL RATES

2.1. Materials and methods

2.1.1. Study area

The study area is located in the Province of Viterbo, northern Latium, central Italy. The area is an hilly landscape ranging between 300-500m asl, where the woodland fragments are surrounded by an agricultural and, to a lesser extent, urban matrix. A relatively simplified network of linear structures, as hedgerows and tree lines, sharps a system of more or less connected woodland fragments. The agricultural matrix is mainly composed by arable fields, olive groves and orchards. During the spring and summer months, fields are cultivated mainly with wheat and corn and, to a lesser extent, *Medicago sativa*.

The fragments may be considered as mixed broadleaved oak woodlands with termophilous and mesophilous species. The dominant arboreal species are *Quercus pubescens* and *Quercus cerris*.

A previous research verified in the study area the presence of the *M. avellanarius* (Mortelliti *et al.* 2011), while the presence of the *M. glareolus* was determined through a pilot survey (March 2011).

Over the study area we superimposed a squared landscape, sized 10 km² (Fig. 2.1), where the sample fragments were selected. The total number of fragments within the squared landscape is 103, while the overall forest cover is less than 10% (762 ha), a threshold of remaining habitat at which the effects of habitat fragmentation *stricto sensu* and of structural connectivity disruption seems to affect animal populations (Fahrig 2003, Mortelliti *et al.* 2011).



Figure 2.1. The fragmented landscape (of 100 km²) selected to investigate the demographic parameters and the population dynamics of the *M. avellanarius* and of the *M. glareolus* populations. Green polygons denotes the woodland fragments.

2.1.2. Study design and sampling protocols

M. avellanarius

Nine woodland fragments were selected for the investigation of the demography and the population dynamics of *M. avellanarius* (Fig. 2.2). Those fragments were previously sampled on 2010 (through a monthly one-day nest-boxes check; Imperi 2010, Santarelli 2011, Fipaldini 2012). However, during the winter of 2010 one fragment (MA5 in Tab. 2.1) was clearcutted. Therefore, while my field work was carried out on the remaining eight fragments, I performed the analysis on the vital rates using the data gathered in the whole period 2010-2012.

Woodland fragments were selected in order to account for a gradient in fragment size ranging from 0,12 ha to 233, 91 ha (Tab 2.1).

Demographic data were gathered by using nest-boxes grids (Juškaitis 2006) fixed on tree trunks at 1-1.5 meters height with the hole facing the trunk. In each sampled woodland a grid of nest-boxes was placed. In woodlands sized 20 hectares or larger we placed a squared grid of about 36 nest-boxes (6 x 6 lines) spaced about 40 meters (Fig. 2.3b); we located these latter grids with the aim to reduce the edge effect on the grid. In smaller woodlands the nest-boxes were placed in all the woodland with the same density specified above (6 nest-boxes per hectare), 40 meters spaced (Fig. 2.3a). A total of 210 nest-boxes were placed in the field (Tab. 2.1).

During 2011-2012, nest-boxes were checked for the presence of *M. avellanarius* every month with the following sampling protocol: at

alternate months all nest-boxes were checked for one day or for three days. In practice, the first month we checked all the nest-boxes only one time; the second month we checked all the nest-boxes three times, once every four days; the third month we checked all the nest-boxes again only one time; the fourth month we checked all the nest-boxes again three times; and so on. On 2010 the checks of nest-boxes were carried out once a month.

All individuals captured were individually marked by PIT (Passive Integrated Transponder; 2010), ear tags (2011) and leg rings (2012; Fig 2.4). Furthermore they were sexed, aged (following the following age classes: offsprings, juveniles, adults), weighed and the reproductive status was determined. Offsprings and juveniles in litters were counted and aged on the base of fur presence and colour and body weight (Fig. 2.5; Juškaitis 2008). Then the individuals were released. A tissue sample was taken for future genetic analyses.

Data gathering of *M. avellanarius* demographic parameters was performed between April 2011 and December 2012. A total of 35 nest-boxes checks were carried out. On 2010 sampling was performed from May to November, for a total of 7 nest-boxes checks.

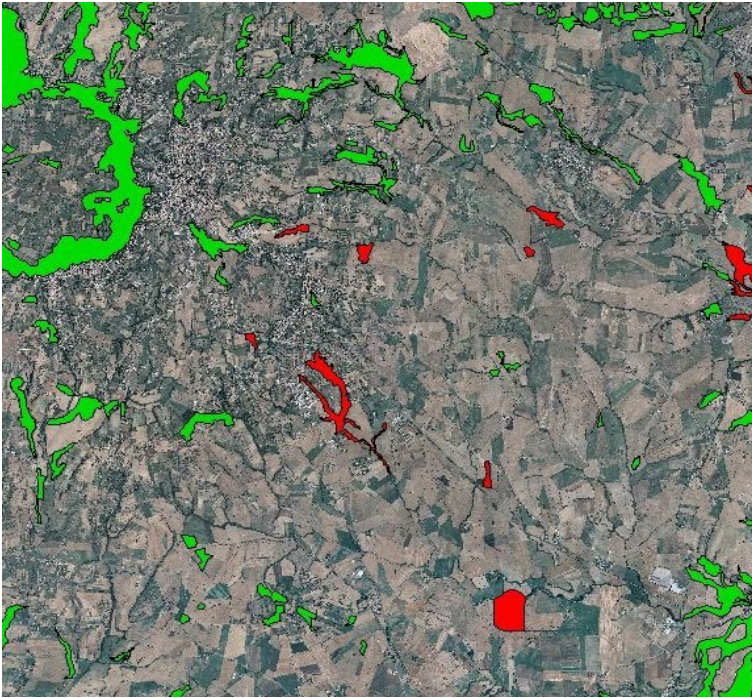


Figure 2.2. The fragmented landscape (of 100 km²) selected to investigate the demographic parameters and the population dynamics of the *M. avellanarius* populations. Green polygons denotes all the woodland fragments in the investigated landscape. Red denotes the woodland fragments selected for population sampling.

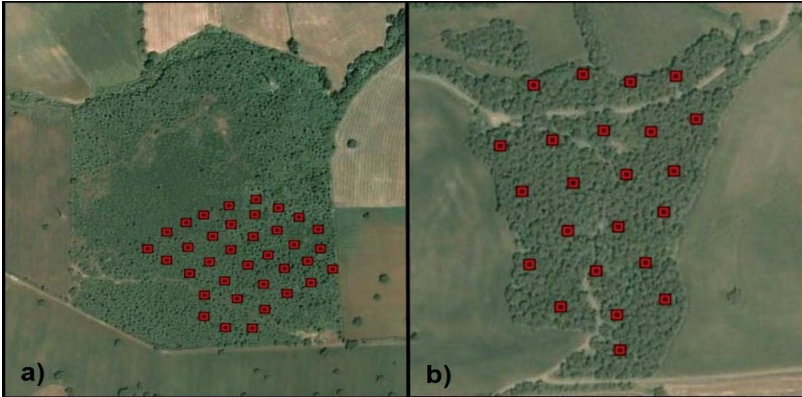


Figure 2.3. The distribution of nest-boxes in the selected woodland fragments: a) in fragments > 20 hectares a squared grid of 36 nest-boxes (6 x 6 lines) spaced 40 meters was positioned; b) the fragments of size < 20 hectares were entirely sampled with a density of 6 nest-boxes per hectare.

Table 2.1. Size of, and number of nest-boxes placed in, each one of the 9 woodland fragments where *M. avellanarius* populations were sampled.

FRAGMENT	SIZE (ha)	Nr. of NEST-BOXES
MA1	233,91	36
MA2	22,03	35
MA3	21,5	36
MA4	5,72	27
MA5	3,8	23
MA6	2,87	17
MA7	2,55	16
MA8	1,74	12
MA9	1,2	8

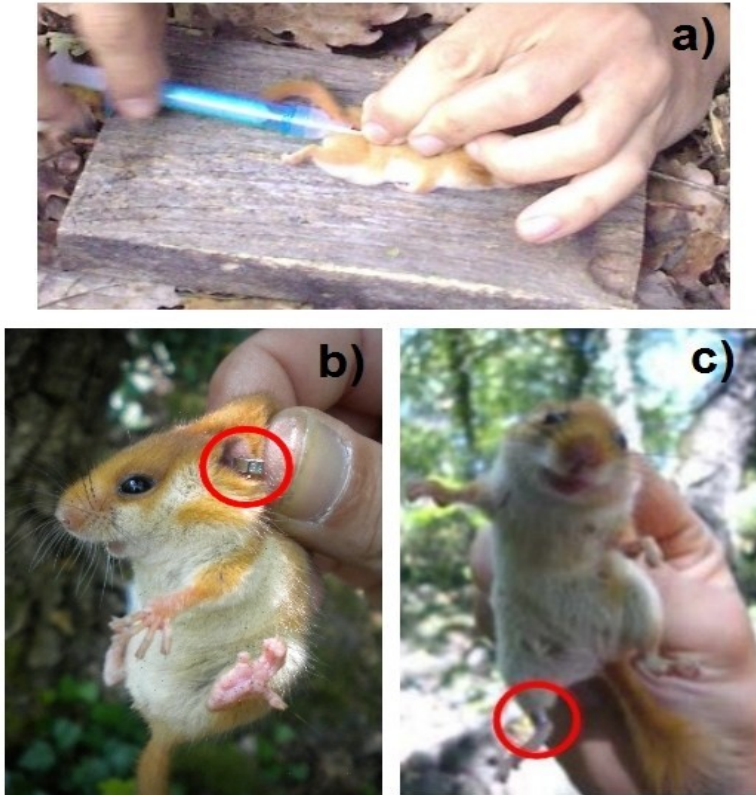


Figure 2.4. Examples of *M. avellanarius* individuals marked with PIT (a), ear tag (b) and leg ring (c).



Figure 2.5. Litter of *M. avellanarius* founded inside a nest-box during a check.

M. glareolus

Demographic parameters and population dynamics of the *M. glareolus* were investigated in 29 woodland fragments (Fig. 2.6).

We strategically selected woodland fragments in order to obtain all possible combination of three factors: 1) the fragment size, 2) the quantity of hedgerows connected to the focal fragments, 3) the density and complexity of the woodland shrub layer. The first factor, fragment size, was classified in four categories: < 2 ha, 2-5 ha, 5-10 ha, 10-25 ha. Moreover, a continuous forest (more than 200 ha in size) was selected as

a control area. Within each of these size categories we further classified the fragments on the basis of: i) the number of hedgerows departing from the focal fragment, and ii) the density of the cover of shrub layer. Each of these two factors were divided in two categories, relatively high and relatively low. The number of connected hedgerows was determined by aerial photographs, while the density of the shrub layer was visually estimated.

Each combination of the three factors was replicated two times depending on patterns availability and logistical constraints. Tab. 2.2 presents all the woodland fragments representing the combination of the three factors exposed above where we carried out the sampling of *M. glareolus* populations.

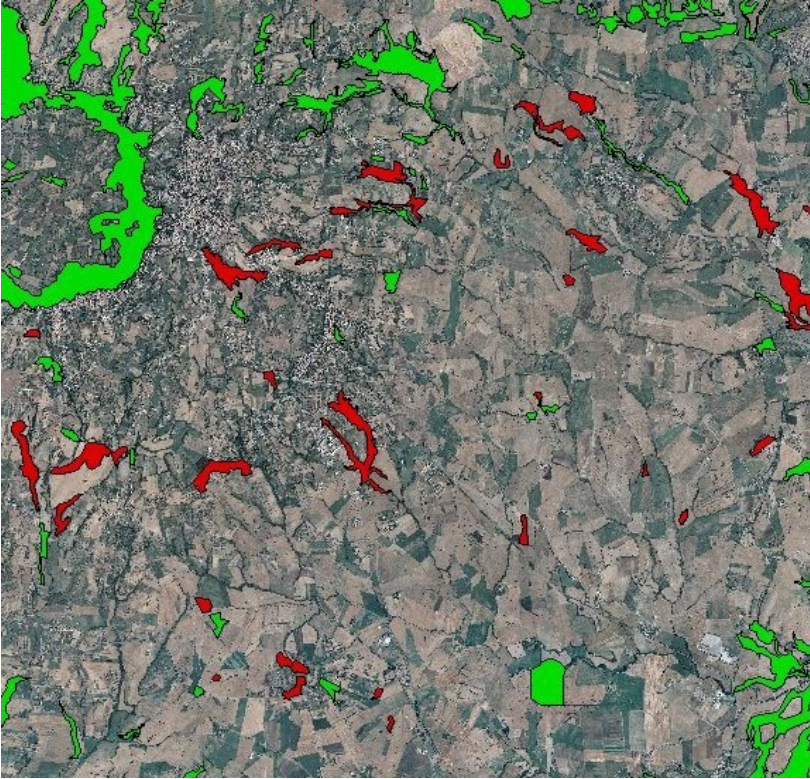


Figure 2.6. The fragmented landscape (of 100 km²) selected to investigate the demographic parameters and the population dynamics of *Myodes glareolus* populations. Green polygons denotes all the woodland fragments in the investigated landscape. Red denotes the woodland fragments selected for population sampling.

Table 2.2. Study design for the sampling of terrestrial rodent populations. We selected 29 woodland fragments on the basis of a combination of three factors: 1) the fragment size (values in brackets); 2) the number of hedgerows departing from the fragment (high/low); 3) the density of the shrub layer (high/low).

PATCH SIZE	Nr. of HEDGEROWS	SHRUB DENSITY	
		High	Low
< 2 ha	High	MG7 (1,203) MG9 (1,594) MG2 (0,752)	
	Low	MG4 (0,880) MG1 (0,563) MG5 (1,012)	MG8 (1,459) MG6 (1,198) MG3 (0,825)
2-5 ha	High	MG14 (2,865) MG11 (2,549)	MG16 (4,387) MG17 (4,717)
	Low	MG12 (2,736) MG13 (2,853)	MG10 (2,255) MG15 (3,538)
5-10 ha	High	MG18 (5,067) MG20 (5,807)	MG21 (7,694) MG22 (9,663)
	Low		MG19 (5,724)
10-25 ha	High	MG27 (17,216) MG24 (11,710)	MG28 (24,785) MG26 (14,076)
	Low	MG23 (10,635)	MG25 (13,646)
> 200 ha		MG29 (233,910)	

Populations of *M. glareolus* were sampled by live-trapping. In each sampled woodland we placed a squared grid with a mix of Sherman and Longworth traps (7x7 traps = 49, trap ratio Sherman/Longworth = 4/1) with 10 m spacing. If the sampled fragment was smaller than 0,36 ha (the standard size of the grids), the entire fragment was sampled, holding constant the trap spacing and the Sherman/Longworth trap ratio.

Every trap grid was activated every two months for three consecutive nights. All individuals captured were individually marked by toe clipping. Furthermore they were sexed, aged (following the following age classes: juveniles, adults), weighted and the reproductive status was determined. Then the individuals were released. Furthermore, we determined the number of pregnancies and the litters size, by counting the number of placental scars (Fig. 2.7; Corthum 1967, Alibhai 1980), in the uteros on females died during the trapping sessions. Twelve trapping sessions were performed, for a total of 47.118 trap-nights. Trapping sessions were carried out from April 2011 to February 2013.



Figure 2.7. Uterus of *M. glareolus* extracted from a female died during a trapping session. The black spots identify the placental scars.

2.1.3. Fragments and neighbourhood characteristics

Patch and patch-landscape explanatory variables. The patch and neighbourhood landscape features (as hedgerows and tree lines) were measured with Arcview 3.3, and “Identify features within distance” extension for Arcview (Jenness 2003), using Corine Land

Cover (with a resolution of 0.1 ha) and digitized aerial photographs as main layers.. Patch-landscape scale metrics were measured in two different buffers surrounding the fragments, one for *M. avellanarius* (497 m) and one for *M. glareolus* (1072 m), through “Patch Analyst” extension for Arcview (<http://flash.lakeheadu.ca/~rrempe/patch/>). The wide of the buffer was determined in two different ways: 1) for *M. avellanarius* was the maximum edge-to-edge distance between a totally isolated fragment (i.e. in absence of connected hedgerows and surrounded only by cultivated fields) where we recorded a colonization and the nearest fragment; 2) for *M. glareolus* was the maximum edge-to-edge distance among the pairs of fragments where we recorded migrations of marked individuals (Tab. 3.2). See Table 2.3 for a complete list of variables measured.

Vegetation structure of woodland fragments. With the aim of characterizing the sampled woodlands in terms of vegetation structure and composition we performed vegetation plots within each sampled fragment. My hypotheses is that different structures of the woodland vegetation, with particular regard to the shrub layer, might determines the availability of important breeding and shelter resources (for example, shrub structure and tree holes and cavities for *M. avellanarius* nesting, and the shrub layer density for *M. glareolus* shelter), and, as a consequence, might affect their vital rates.

Patch structure variables were measured in quadrat plots 10x10m sized. The number of plots was proportional to patch size and the location of each plot was randomly determined. In order to estimate

plant cover we applied a modified Braun Blanquet method. See Table 2.3 for a complete list of variables recorded. Vegetation structure sampling were performed during May 2012.

Oak productivity. In the study area the majority of the woodland fragments are managed for timber production. This type of management occurs at different time lags (i.e. every 10 or 15 years), determining a variable age among fragments. Moreover, in fragments larger than 5 hectares the management usually occurs at different time lags in different parts of the stand. This type of management has consequences on the age, size and, we hypothesize, acorn productivity of the oaks. My hypotheses is that the different acorn availability among fragments might determine different responses of rodent populations, in particular different effects on demographic parameters as survival rate and fertility.

In order to estimate the woodland productivity in terms of acorn biomass, in each grid sampled for terrestrial rodents 2 areas of 400 m² were delimited and all productive oaks (belonging to the species *Q. cerris* and *Q. pubescens*) inside the areas were identified and the canopy area estimated. Below each productive oak, 2 circular plots with 1 meters of diameter were placed. In each plot, all acorns were counted and weighed, then 10% of the total number of acorns counted or at least 10 acorns were taken. Subsequently, these samples were dehydrated in laboratory in order to obtain the dry weight. This parameter were elaborated with an estimate of the canopy cover of the oaks where the samples were taken. Then an estimate of *Q. cerris* and *Q. pubescens* acorns mass available in the fragment were elaborated.

Data collection on oak productivity was performed on November-December 2012 and repeated on November-December 2013.

In Appendix I are reported the fragment values of each covariate.

Table 2.3. List of covariates used as predictor variables for the CJS and linear regression models of *M. avellanarius* and *M. glareolus* survival rates and fertilities.

Covariate Type	List of covariates	
Fragments and neighborhood characteristics	logha	Log ₁₀ of fragment size in hectares
	par	Perimeter-area ratio
	neardist	Distance of the nearest fragment (m)
	ha_pch_con	Total hectares of connected fragments (ha)
	pch_con	Number of connected fragments
	ha_buff497	Total hectares of habitat within a buffer of 497 m (ha)
	ha_buff721	Total hectares of habitat within a buffer of 1072 m (ha)
	pch_buff497	Number of fragments within a buffer of 497 m
	pch_buff721	Number of fragments within a buffer of 1072 m
	hdg_con	Number of hedgerow s connecting to the fragment to other fragments
	hdgxpch	Number of hedgerow s connected to the fragment
log_sem	Log ₁₀ of hectares of arable fields within a buffer of 1072 m	
Vegetation structure	nalb	Mean number of trees in 100 m ²
	canopy	Index of tree canopy cover
	mdbh	Mean tree trunk diameter at breast height
	volshr	Index of volume of the shrub layer
	rich	Richness of the shrub layer
	shan	Shannon diversity index of the shrub layer
	erb	Index of the herbaceous cover
	lett	Index of the leaf litter cover
Food resource	nshr	Mean number of shrub species in 100 m ²
	abshr	Index of the cover of fruit-bearing shrubs
	abshr_sel	Index of the cover of selected fruit-bearing shrubs
	ruscus	Index of <i>Ruscus aculeatus</i> cover
	rubus	Index of <i>Rubus</i> spp cover
	prunus	Index of <i>Prunus</i> spp cover
	rosa	Index of <i>Rosa canina</i> cover
	crataegus	Index of <i>Crataegus</i> spp cover
	ligustrum	Index of <i>Ligustrum vulgare</i> cover
	cornus	Index of <i>Cornus</i> spp cover
	gh_cer	Dehydrated mass of <i>Q. cerris</i> acorns (kg)
	gh_rov	Dehydrated mass of <i>Q. pubescens</i> acorns (kg)
	gh_tot	Sum of gh_cer and gh_rov

2.1.4. Data analysis

In order to analyse and describe the demographics and the population dynamics of *M. avellanarius* and *M. glareolus* in the area here investigated, I estimated for both species the vital rates, i.e. the survival rate and the fertility, and calculated the population density and sex ratio in each fragment.

For the estimation of the survival rates of *M. avellanarius* I used also the data gathered in the same fragments during the year 2010, plus fragment MA5 (Tab. 2.1; Imperi 2010, Santarelli 2011, Fipaldini 2012). All others parameters were estimated or calculated by using the data gathered in the period 2011-2012.

Density and sex ratio. In order to describe the demography and dynamics of the populations of *M. avellanarius* and *M. glareolus* in the woodland fragments investigated in this research, I calculated, for each fragment, the density and the sex ratio. Those two demographic parameters were estimated using only the data gathered in the period 2011-2012 for *M. avellanarius* and the period April 2011 – February 2013 for *M. glareolus*.

Density was calculated for each sampling session with the following formula:

$$d_t = N_t / Ha$$

where d_t is the fragment density in the sampling session t , N_t is

the number of individuals captured during the sampling session t (the minimum number of individuals known to be alive during the sampling period t) and Ha is the fragment size in hectares. Since the different sampling protocols adopted to capture the two species, the methods used to determine the values in the numerator also differ. For *M. avellanarius* I considered only the individuals captured during the first day of each nest-boxes check (offsprings excluded), both in the single-day sessions and in the three-days sessions. For *M. glareolus* I considered all the individuals marked during the three night-trap of each trapping session.

Finally, for both species I estimated the sex ratio in every fragment through the male-female ratio.

Survival rate. I modelled the capture history (a series of 1 = capture / 0 = no capture) of the individuals marked as a function of the explanatory variables through capture-mark-recapture Cormack-Jolly-Seber (CJS) models. CJS models allows the estimate of the survival probabilities $surv$, accounting for variability in capture probabilities p .

For *M. avellanarius* I used the capture history of all individuals marked, while for *M. glareolus*, since the great dataset, I modelled only the capture history of females.

In order to consider the problem of collinearity when two or more covariates are tested in the same model (Tabachnick & Fidell 2007), I tested the correlation among the selected variables. Since quite all the variables showed significant bivariate correlations (Appendix II), I fitted only models with the survival probability as a function of one covariate.

CJS models were fitted using the software MARK (White &

Burnham 1999; <http://www.phidot.org/software/mark/>).

I followed an information-theoretic approach for model selection and inference. Models were first ranked according to AICc (second order Akaike Information Criterion; Akaike 1973) values. Then, in order to make inference with the best supported set of candidate models, I selected the models with $\Delta\text{AICc} < 1$ and recalculated the Akaike weights (AICc w ; Burnham & Anderson 2002).

Fertility. As mentioned above (Par. 2.1.2) two different types of data sources were used to obtain the estimates of the fertilities of *M. avellanarius* and *M. glareolus*: the litter size recorded during the nest-boxes checks for *M. avellanarius* (Fig. 2.5), and the count of pregnancies and placental scars for *M. glareolus* (Fig. 2.7).

I modelled these estimates of the fertility as a function of the explanatory variables through linear regression models using the statistical software SPSS (SPSS Inc., Chicago, IL, USA). Due to the collinearity among many covariates, I fitted only models with the fertility as a function of one covariate. The litters of *M. avellanarius* found during the nest-boxes checks might vary in the age (Juškaitis 2008): they could be composed either by hairless, blind and static offsprings or by hairy and mobile juveniles. Due to the offspring and juvenile mortality, the initial litter size might change through time. In order to statistically control this potential source of sample error, I imposed in each fitted model a binary covariate (AGE): 1 = offspring, 2 = juvenile.

Similarly, since in *M. glareolus* populations the number of

pregnancies and the litter size might be subjected to year-to-year fluctuations in climate and vegetation conditions (Oksanen et al. 2001, Koivula et al. 2003), in the analysis of *M. glareolus* fertility I imposed in each tested model a binary covariate (YEAR: 1 = April 2011 – February 2012, 2 = April 2012 – February 2013), representing the year in which the female individual died during a trapping session and the utero was collected.

As in the case of the analysis of survival rate, I followed an information-theoretic approach for model selection. Models were first ranked according to AIC (first order Akaike Information Criterion; Akaike 1973) values.

Then, in order to make inference with the best supported set of candidated models, I selected the models with $\Delta\text{AICc} < 1$ and recalculated the Akaike weights (AICc w ; Burnham & Anderson 2002). Nagelgerke R^2 were used as a measure of the goodness-of-fit.

2.2. Results

2.2.1. *M. avellanarius*

Over the entire study period 2010-2012 *M. avellanarius* were detected in all the investigated fragments. A total of 163 adult and subadult individuals (2010 = 26, 2011 = 88 and 2012 = 49), and 72 offsprings and juvenils (2010 = 9, 2011 = 53 and 2012 = 10; Fig. 2.8)

were captured.

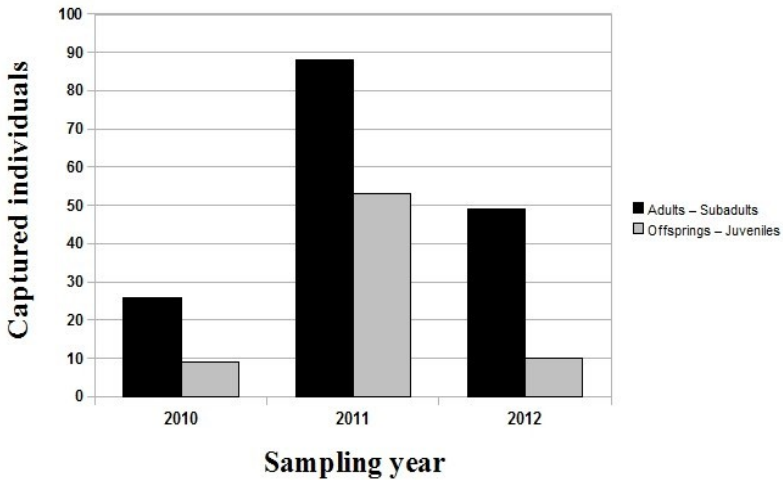


Figure 2.8. Total number of individuals of *M. avellanarius* captured over the entire study period, showed by year.

Density

The mean density values calculated on the entire study period showed that fragments of bigger and smaller size presents higher densities, with maximum values in fragments MA8 (0,5 ind/ha) and MA7 (0,49 ind/ha; Fig. 2.9). At the opposite, lower densities (range: 0,01-0,15 ind/ha) were recorded in fragments of middle size (from MA4

to MA7; Fig. 2.9).

Although the temporal trend of this parameter tend to vary from fragment to fragment (Fig. 2.10), higher density values were recorded during two seasons: spring and autumn. In particular, the higher density was found on autumn 2011 and autumn 2012 (respectively in fragment MA3 = 10,73 ind/ha, and in fragment MA2 = 7,12 ind/ha; Fig. 2.10). In summer the densities never exceeded 1,53 ind/ha (on summer 2012 in fragment MA9).

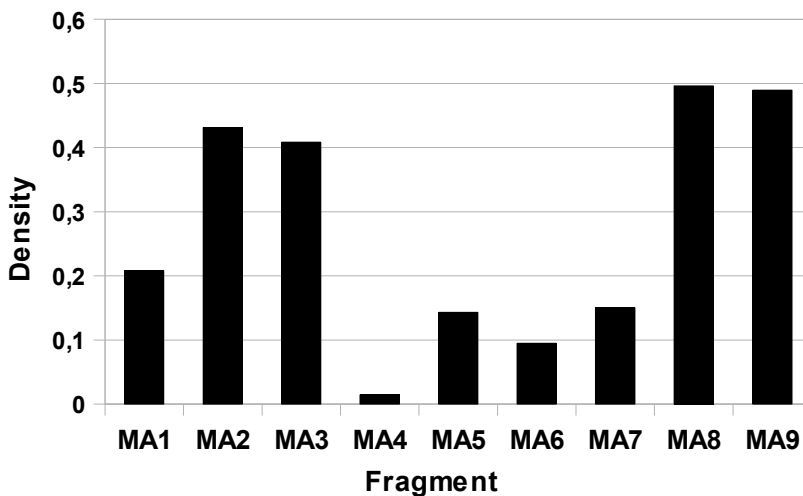


Figure 2.9. Mean density values of *M. avellanarius* recorded in each fragment during the entire study period.

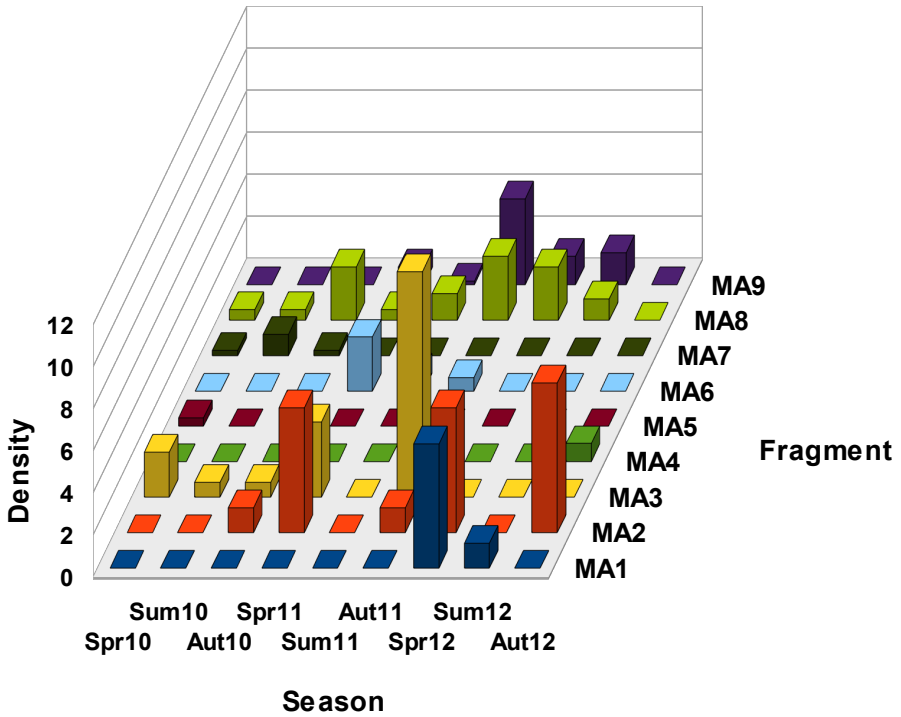


Figure 2.10. Seasonal variation of density values of *M. avellanarius* recorded in each fragment during the entire study period.

Sex ratio

The number of adult and subadult males was 31 on year 2011 and 23 on year 2012, while we captured 40 adult and subadult females on

year 2011 and 22 on year 2012 (Fig. 2.11). The discrepancies between the total individuals captured in a year and the sum of male and female of the same year (Fig. 2.8) was due to the difficulty to identify the sex of some individuals. For the same reason I did not considered the male-female ratio of the data gathered on year 2010.

Therefore, the sex ratio of the entire study area in the year 2011 was 0,78, while in the year 2012 the sex ratio was 1,05.

At the fragment level the sex ratio was very variable both among fragmens and in the same fragment between years (Fig. 2.12). As an example, in fragment MA2 the sex ratio shifted from 0,5 of the 2011 to 1,5 of the 2012 (Fig. 2.12).

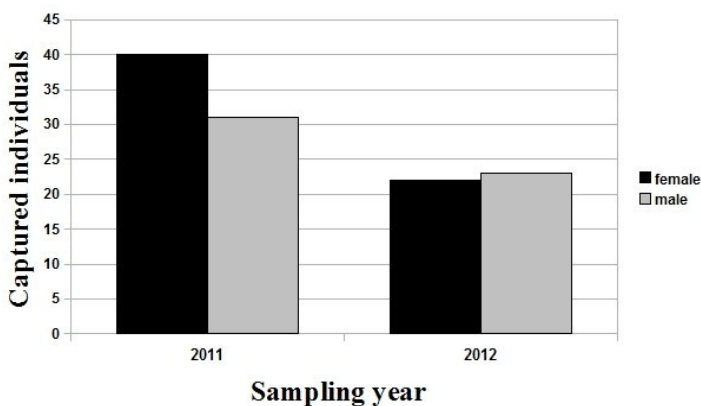


Figure 2.11. Total number of male and female *M. avellanarius* individuals captured during 2011 and 2012.

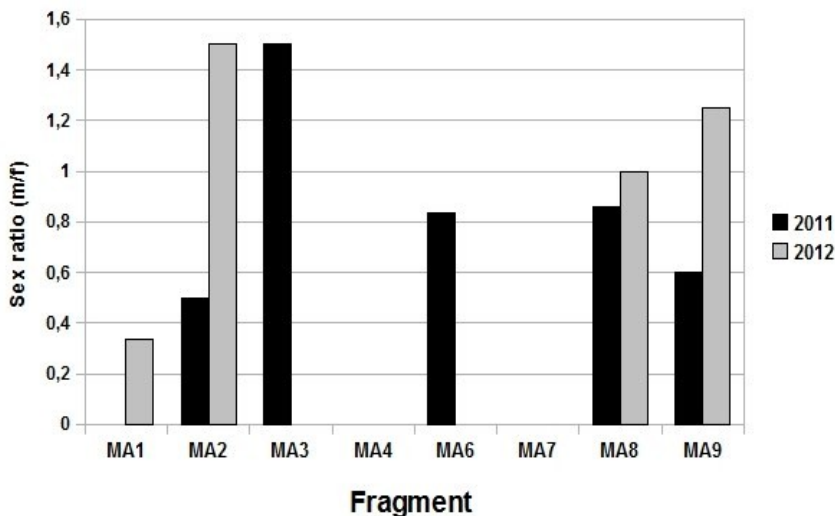


Figure 2.12. Annual male-female ratio of *M. avellanarius* in each of the investigated fragments captured during 2011 and 2012.

Survival rate

In the first ranked model *surv* (survival probability) was modeled as a function of the mean number of shrub individuals in 100 m² (nshr; Tab. 2.4). The estimated survival probability was 0,0011 (st.dev. = 0,0006; Tab. 2.5). Capture probability (*p*) was affected: i) by the season when the nest-box check occurs (season), with lower values in summer; ii) by the mean fragment abundance of *M. avellanarius* (abpch

in Tab. 2.4) with higher values at lower mean abundances (Tab. 2.5). The weight of this model was 1, therefore I adopted the first model for inferences. In Tab. 2.5 are reported the *beta* values for the first ranked model.

Table 2.4. Summary of the CJS models fitted to estimate the survival probability of *M. avellanarius*. The CJS models are ranked according to AICc (second order Akaike Information Criterion). ΔAICc = difference between the model with lowest AICc and the given model; $\text{AICc } w$ = Akaike weights; season = season when nest-boxes check was carried out (summer/other seasons), abpch = mean fragment

Model	AICc	ΔAICc	$\text{AICc } w$
<i>surv</i> (nshr), <i>p</i> (season,abpch)	1726,5	0	1
<i>surv</i> (hdgxpch), <i>p</i> (season,abpch)	1739,93	13,43	0
<i>surv</i> (nalb), <i>p</i> (season,abpch)	1748,67	22,17	0
<i>surv</i> (rich), <i>p</i> (season,abpch)	1755,01	28,51	0
<i>surv</i> (ha_buff497), <i>p</i> (season,abpch)	1768,06	41,56	0
<i>surv</i> (pch_buff497), <i>p</i> (season,abpch)	1776,77	50,28	0
<i>surv</i> (ha_pch_con), <i>p</i> (season,abpch)	1779,31	52,81	0
<i>surv</i> (cost), <i>p</i> (season,abpch)	1783,28	56,78	0
<i>surv</i> (can), <i>p</i> (season,abpch)	1784,13	57,63	0
<i>surv</i> (logha), <i>p</i> (season,abpch)	1784,8	58,31	0
<i>surv</i> (cost), <i>p</i> (season,logha)	1876,78	150,28	0
<i>surv</i> (cost), <i>p</i> (season,dens)	1888,47	161,97	0
<i>surv</i> (cost), <i>p</i> (season)	1893,76	167,26	0
<i>surv</i> (cost), <i>p</i> (cost)	1911,2	184,7	0
<i>surv</i> (pch_con), <i>p</i> (season,abpch)	1958,44	231,95	0

abundance.

Table 2.5. Summary of the parameter estimates and parameter *beta* of the first ranked CJS model. *surv* = survival probability, *p* = capture probability, cost = constant.

Parameter	Covariate	Estimate (S.E.)	
<i>surv</i>		0,0011	(0,0006)
<i>p</i> (summer)		0,039	(0,008)
<i>p</i> (other seasons)		0,076	(0,007)
<i>surv</i>	cost	- 6,78	(0,59)
	nshr	3,58	(0,65)

Fertility

We recorded a total of 22 reproductive events in five fragments (Appendix III, Tab. 1). The mean litter size in the entire study area was 3.3 (s.d. = 1.64). Taking in account the different age of the litter, the mean litter size of litters only with offsprings was 3.8 (s.d. = 1.75), while litters composed by juveniles had a mean value of 2.8 (s.d. = 1.47).

The AIC ranking of the fitted models showed two models within $\Delta AIC < 1$ (Tab. 2.6). In the first ranked model fertility was modelled as

a function of the age class of the litter (AGE), and of the mean number of shrub individuals in 100 m² (nshr). In the second ranked model fertility was a function of AGE and of the index of the cover of the fruit-bearing shrubs (abshr). I adopted those two models for inference; in Tab. 2.7 are showed the parameters estimates of the averaged model.

Table 2.6. Summary of the linear regression models fitted to estimate the fertility of *M. avellanarius*. The models are ranked according to AIC (first order Akaike Information Criterion). RSS = residual sum of squares, Δ AIC = difference between the model with lowest AIC and the given model; AIC w = Akaike weights; R^2 = measure of the goodness-of-fit, AGE = litter age class (offsprings/juveniles).

Model	RSS	AIC	Δ AIC	AIC w	R^2
AGE + nshr	36,59	12,86	0	0,12	0,35
AGE + abshr	37,72	13,15	0,29	0,1	0,33
AGE + shan	40,87	13,92	1,06	0,07	0,27
AGE + rich	40,94	13,93	1,07	0,07	0,27
AGE	51,27	14,08	1,22	0,06	0,09
AGE + pch_con	42,57	14,31	1,45	0,06	0,25
AGE + volshr	42,98	14,4	1,54	0,05	0,24
AGE + hdgxpch	44,34	14,7	1,84	0,05	0,21
AGE + mdbh	45,19	14,88	2,02	0,04	0,2
AGE + pch_buff497	45,71	14,99	2,13	0,04	0,19
AGE + ha_buff497	45,84	15,01	2,15	0,04	0,19
AGE + rubus	46,33	15,12	2,26	0,04	0,18
AGE + ha_pch_con	46,61	15,17	2,31	0,04	0,17
AGE + rosa	46,73	15,2	2,34	0,04	0,17
AGE + hdg_con	46,98	15,25	2,39	0,04	0,17
AGE + crataegus	48,85	15,62	2,76	0,03	0,13
AGE + abshr_sel	49,35	15,72	2,86	0,03	0,13
AGE + comus	49,56	15,76	2,9	0,03	0,12
AGE + prunus	49,96	15,84	2,98	0,03	0,11
AGE + neardist	50,63	15,96	3,1	0,02	0,1
AGE + logha	51,25	16,08	3,22	0,02	0,09
AGE + ligustrum	51,26	16,08	3,22	0,02	0,09

Table 2.7. Summary of the parameter estimates of the averaged model. cost = constant, AGE = litter age class (offsprings/juveniles).

Covariate	Estimate (S.E.)	
cost	- 5,37	(3,89)
AGE	- 0,8	(0,6)
nshr	0,62	(0,23)
abshr	0,45	(0,17)

2.2.2. *M. glareolus*

During the entire study period *M. glareolus* were detected in all but two of the 29 investigated fragments (MG25 and MG26, Tab. 2.2). Were marked a total of 1129 individuals for a total of 2000 capture events (Fig. 2.13). Adult individuals marked were 920 (2011 = 420, 2012 = 500), subadults were 162 (2011 = 67, 2012 = 95) and juveniles were 28 (2011 = 11, 2012 = 17; Fig. 2.14).

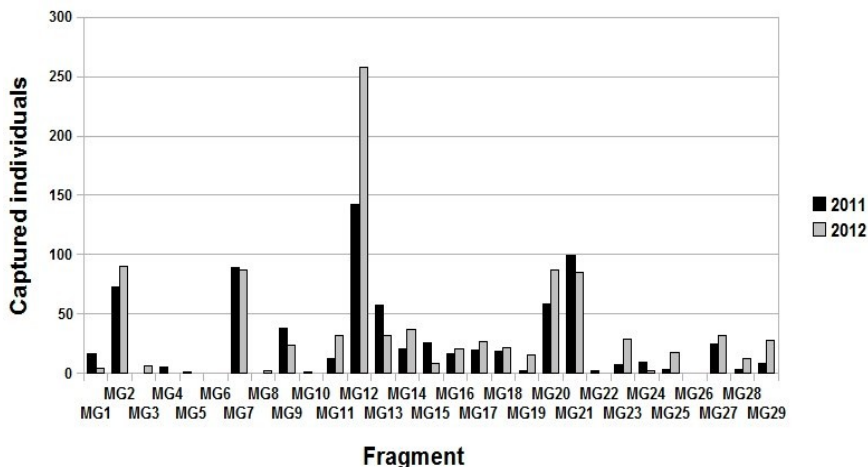


Figure 2.13. Total number of individuals of *M. glareolus* captured in each investigated fragment on 2011 (black) and on 2012 (grey).

Density

The mean density values of *M. glareolus* showed a great variability among fragments (range 0 – 122,2 ind/ha; Fig. 2.15). The year-to-year trend presents 11 fragments where occurred an increase in mean density values, while in 16 fragments the mean density decrease between the first and the second sampling year (Fig. 2.15).

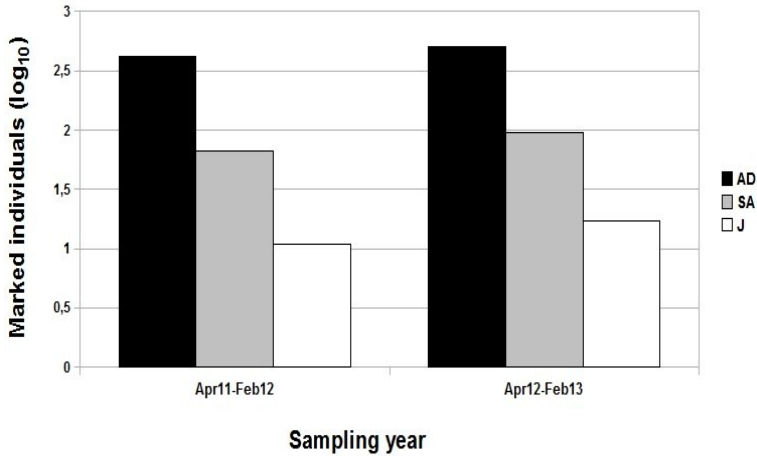


Figure 2.14. Age structure of the *M. glareolus* metapopulation in the two years of the study. Bars represent the \log_{10} -transformed total number of individuals marked of the three age classes (adult AD, subadult SA, and juvenile J).

Sex ratio

During the trapping period April 2011 – February 2012 the total number of males marked was 289 while the total number of females was 342; in the trapping period April 2012 – February 2013 the number of males marked was 425 and the number of females was 410 (Fig. 2.16). The discrepancies between the total individuals captured in a year and the sum of male and female of the same year was due to the difficulty to identify the sex of some individuals, especially for the juveniles.

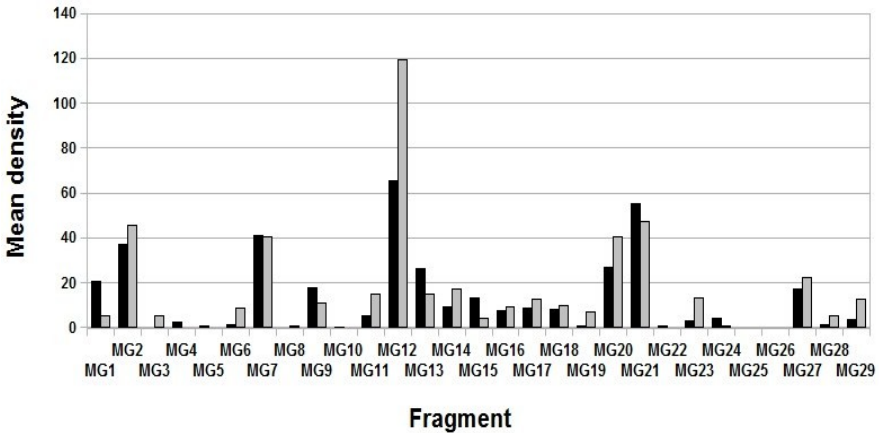


Figure 2.15. Mean density values of *M. glareolus* recorded in each fragment during sampling period April 2011 – February 2012 (black bars) and April 2012 – February 2013 (grey bars).

The sex ratio of the entire study area in the period April 2011 – February 2012 was 0,85, while in the period April 2012 – February 2013 the sex ratio was 1,04.

At the fragment level the sex ratio showed a great variability, both among fragments and in the same fragment between years (Fig. 2.17). As an example, in fragment MG15 the sex ratio shifted from 14 to 5 between the two sampling years (Fig. 2.17).

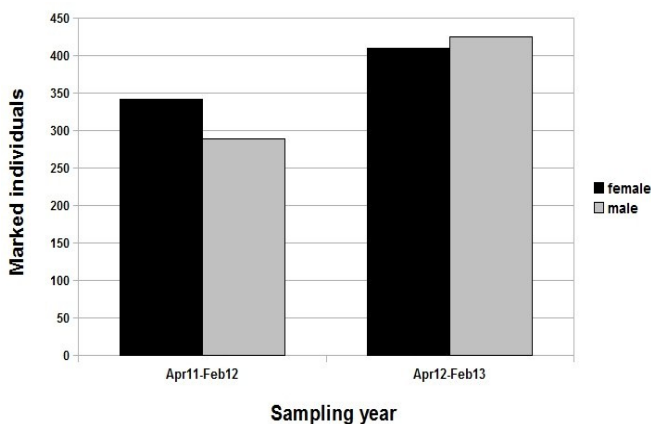


Figure 2.16. Total number of male and female *M. glareulus* individuals marked during the first and the second sampling years.

Survival

In the first ranked model *surv* (survival probability) was modeled as a function of the log₁₀-transformed fragment size in hectares (logha; Tab. 2.7). The estimated survival probability was 0,012 (st.dev. = 0,04; Tab. 2.8). Capture probability (*p*) was time-dependent (i.e. vary among trapping sessions) with the probability of capture in the second and third day of each trapping session constant (*c* cost in Tab. 2.7). Since all other fitted models showed a $\Delta AICc > 1$, I adopted the first model for

inferences. In Tab. 2.8 are reported the *beta* values for the first ranked model. The negative value of the beta of the log₁₀ covariate showed that the survival probability of that species decrease at increasing fragment size.

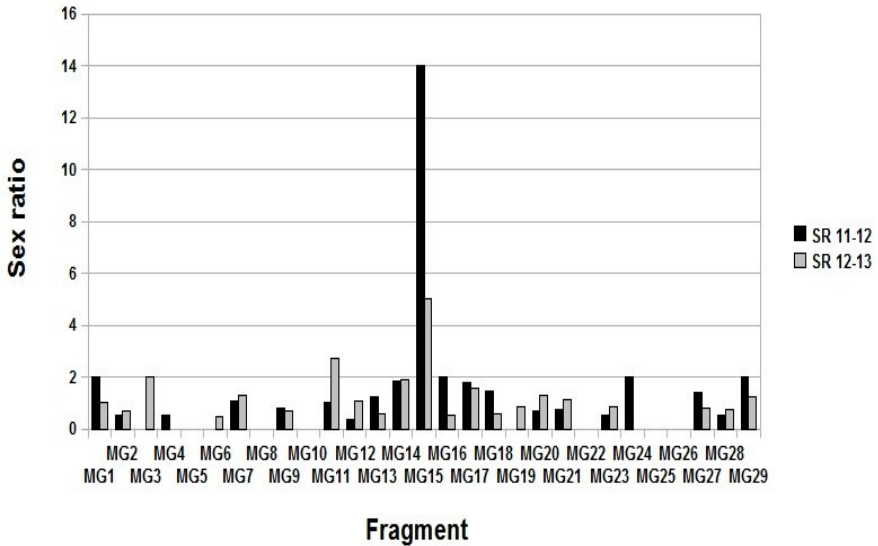


Figure 2.17. Annual male-female ratio of *M. glareolus* in each of the investigated fragments. SR = sex ratio.

Table 2.7. Summary of the CJS models fitted to estimate the survival probability of *M. glareolus*. The CJS models are ranked according to AICc (second order Akaike Information Criterion). ΔAICc = difference between the model with lowest AICc and the given model; AICc w = Akaike weights; cost = constant, $p(t - c \text{ cost})$ = time-dependent capture probability with capture probabilities in the second and third trap-nights of each trapping session constant..

Model	AICc	ΔAICc	AICc w
<i>surv</i> (logha), $p(t - c \text{ cost})$	2210,55	0	0,54
<i>surv</i> (gh_rov), $p(t - c \text{ cost})$	2212,55	2,01	0,2
<i>surv</i> (pch_con), $p(t - c \text{ cost})$	2216,06	5,51	0,03
<i>surv</i> (nalb), $p(t - c \text{ cost})$	2216,08	5,53	0,03
<i>surv</i> (ha_buff721), $p(t - c \text{ cost})$	2216,36	5,81	0,03
<i>surv</i> (cost), $p(t - c \text{ cost})$	2217,45	6,91	0,02
<i>surv</i> (erb), $p(t - c \text{ cost})$	2218,07	7,53	0,01
<i>surv</i> (neardist), $p(t - c \text{ cost})$	2218,13	7,58	0,01
<i>surv</i> (can), $p(t - c \text{ cost})$	2218,17	7,62	0,01
<i>surv</i> (narb), $p(t - c \text{ cost})$	2218,63	8,08	0,01
<i>surv</i> (hdgxpch), $p(t - c \text{ cost})$	2218,95	8,41	0,01
<i>surv</i> (lett), $p(t - c \text{ cost})$	2218,98	8,44	0,01
<i>surv</i> (gh_tot), $p(t - c \text{ cost})$	2219,04	8,49	0,01
<i>surv</i> (volshr), $p(t - c \text{ cost})$	2219,06	8,51	0,01
<i>surv</i> (rich), $p(t - c \text{ cost})$	2219,23	8,69	0,01
<i>surv</i> (pch_buff721), $p(t - c \text{ cost})$	2219,41	8,86	0,01
<i>surv</i> (par), $p(t - c \text{ cost})$	2219,47	8,92	0,01
<i>surv</i> (mdbh), $p(t - c \text{ cost})$	2219,48	8,94	0,01
<i>surv</i> (log_sem), $p(t - c \text{ cost})$	2219,56	9,01	0,01
<i>surv</i> (gh_cer), $p(t - c \text{ cost})$	2219,57	9,02	0,01
<i>surv</i> (abshr), $p(t - c \text{ cost})$	2219,58	9,03	0,01
<i>surv</i> (shan), $p(t - c \text{ cost})$	2219,58	9,04	0,01
<i>surv</i> (cost), $p(t)$	2225,96	15,41	0
<i>surv</i> (cost), $p(t - lett)$	2264,26	53,71	0
<i>surv</i> (cost), $p(t - logha)$	2266,51	55,96	0
<i>surv</i> (cost), $p(c \text{ cost})$	2319,39	108,84	0
<i>surv</i> (cost), $p(cost)$	2362,85	152,3	0

Table 2.8. Summary of the parameter estimates and parameter's *beta* of the first ranked CJS model. *surv* = survival probability, p_x = capture probability of the first day of the *x* trapping session, c_x = capture probability of the second and third day of the *x* trapping session, *cost* = constant.

Parameter	Covariate	Estimate (S.E.)
<i>surv</i>		0,012 (0,004)
c_1		0,42 (0,07)
p_2		0,69 (0,09)
c_2		0,37 (0,05)
p_3		0,29 (0,07)
c_3		0,36 (0,05)
p_4		0,49 (0,1)
c_4		0,16 (0,05)
p_5		0,42 (0,11)
c_5		0,16 (0,05)
p_6		0,17 (0,08)
c_6		0,11 (0,03)
p_7		0,33 (0,07)
c_7		0,12 (0,02)
p_8		0,16 (0,04)
c_8		0,06 (0,02)
p_9		0,13 (0,04)
c_9		0,08 (0,02)
p_{10}		0,33 (0,07)
c_{10}		0,16 (0,03)
p_{11}		0,21 (0,06)
c_{11}		0,07 (0,02)
p_{12}		0,29 (0,08)
c_{12}		0,05 (0,02)
<i>surv</i>	<i>cost</i>	- 4,4 (0,34)
	<i>logha</i>	- 1,11 (0,43)

Fertility

We collected 34 uteros coming from nine fragments, where we detected a total of 44 placental scars (Appendix III, Tab. 2). The mean value of fertility in the entire study area was 3.39 (s.d. = 1.77), with a slight difference between the mean value of the first sampling year, 3.7 (s.d. = 1.56), and the mean value of the second sampling year, 3.12 (s.d. = 1.95).

The results of the linear regression analyses showed only one model with $\Delta AIC < 1$ (Tab. 2.9). In the first ranked model the fertility of *M. glareolus* was modelled as a function of the year in which the utero was collected (YEAR), and of the mean number of shrub individuals in 100 m^2 (nshr).

In Tab. 2.10 are reported the *beta* values for the first ranked model. The negative value of the beta of the nshr covariate showed that the fertility of that species decrease at increasing mean number of shrub individuals.

Table 2.9. Summary of the linear regression models fitted to estimate the fertility of *M. glareolus*. The models are ranked according to AIC (first order Akaike Information Criterion). RSS = residual sum of squares, Δ AIC = difference between the model with lowest AIC and the given model; AIC w = Akaike weights; R^2 = measure of the goodness-of-fit, YEAR = year in which the female individual died during a trapping session.

Model	RSS	AIC	Δ AIC	AIC w	R^2
YEAR + nshr	99,63	23,62	0	0,3	0,23
YEAR + abshr	105,57	24,72	1,11	0,17	0,18
YEAR + mdhb	119,63	27,11	3,5	0,05	0,07
YEAR + can	120,24	27,21	3,59	0,05	0,07
YEAR + nalb	120,36	27,23	3,61	0,05	0,07
YEAR + gh_cer	120,9	27,31	3,7	0,05	0,06
YEAR + par	122,72	27,6	3,98	0,04	0,05
YEAR + rich	122,85	27,62	4	0,04	0,05
YEAR + shan	123,81	27,77	4,15	0,04	0,04
YEAR + gh_rov	124,59	27,89	4,27	0,04	0,03
YEAR + pch_con	126,6	28,2	4,58	0,03	0,02
YEAR + logha	127,01	28,26	4,64	0,03	0,02
YEAR + hdg_con	127,02	28,26	4,64	0,03	0,02
YEAR + volshr	127,28	28,3	4,68	0,03	0,01
YEAR + hdgxpch	127,3	28,3	4,68	0,03	0,01
YEAR + gh_tot	127,39	28,31	4,7	0,03	0,01

Table 2.10. Summary of the parameter estimates of the averaged model. cost = constant, YEAR = year in which the female individual died during a trapping session.

Covariate	Estimate (S.E.)
cost	8,84 (1,6)
YEAR	- 0,62 (0,5)
nshr	- 0,51 (0,15)

3. SEPMs AND OPTIMAL CONSERVATION STRATEGIES

In the present chapter I will: i) describe the procedures I adopted to parameterize and build the SEPMs for the *M. avellanarius* and *M. glareolus* metapopulations (**SEPMs parameterization** section); ii) expose the results of the PVA carried out (**RAMAS population viability analysis** section). Following the PVA results, I elaborated and implemented, for each species, the simulation protocols direct to detect the optimal conservation strategies for the long term persistence of the species in the investigated landscape (**Simulation protocols and optimal conservation strategies** section).

It is important to note that in RAMAS the term “metapopulation” refers to any spatially structured population, not only the classic metapopulation previously defined (see Chap. 1, Par. 1.5). In order to approach a terminology as coherent as possible, and since the real dynamics of the metapopulations of the two investigated species are unknown, in the present chapter I will refer to a metapopulation as a system of several populations spatially distributed within the landscape under investigation.

3.1. SEPMs parameterization

A spatially explicit population model (SEPM) is a model that carry out a population viability analysis, linking demographic data of a species with the spatial data of the habitat requirements of that species.

RAMAS GIS is a software that links GIS-generated landscape data to a metapopulation model (Akçakaya 2005). It combines spatial data on the landscape with habitat requirements of a species and demographic data on its population dynamics into a metapopulation model. This model can be run to simulate future changes in the abundance of the species and its distribution in the landscape, to estimate the metapopulation viability, the risk and time of extinction or decline.

The RAMAS GIS software consists of five programs. In the present research I used only two programs: the **Spatial Data program** and the **Metapopulation Model program**.

The Spatial data program uses spatial data on habitat requirements of a species, such as GIS-generated maps of land uses and habitat vegetation characteristics. It combines these data into a map of habitat suitability with a user-defined function, a map that is used by the program to find habitat fragments where the habitat is suitable and the species might survive. In practice, the program determines the spatial structure of a metapopulation and calculate the demographic parameters in each fragment. Both the spatial structure and the demographic parameters are saved as input for the Metapopulation Model program.

With the Metapopulation Model program is possible to build

stage-structured, spatially explicit metapopulation models and to run simulations with these models. The results of these simulations are the prediction of the extinction or decline risk, the time to extinction, the expected metapopulation abundance, its variation and spatial distribution.

In the present research I built, for each species, one-stage, only-females stochastic metapopulation models. In the following section I will list and define (as defined in the RAMAS GIS tutorial), divided for each program, the RAMAS features and parameters I used to built the metapopulation models. For each feature or parameter I will explain how it was obtained for both *M. avellanarius* and *M. glareolus* (Tab. 3.1).

Table 3.1. List of features and parameters, and relatives parameterizations, used in the present research to build the metapopulation models for the two investigated species.

Parameter	<i>M. avellanarius</i>
Input maps	[nshr], [abshr]
Habitat suitability (HS) function	[nshr]
HS threshold	[nshr] = 6.53
Neighborhood distance	1
Carrying capacity (K)	(1.16/100) * 0.53 * (noc)
Standard deviation of K	0.9
Initial abundance (N ₀)	(0.66/100) * 0.53 * (noc)
Maximum growth rate (R _{max})	1.04
Relative fecundity	(-5.37 + 0.62*[nshr] + 0.45*[abshr]) * 0.53 * 1.5
Relative survival	$\exp(-6.78 + 3.58*[nshr]) / (\exp(-6.78 + 3.58*[nshr]) + 1)$
Density dependence	Scramble
Dispersal-distance function	$m_{ij} = 0.01 * \exp(-D_{ij}^1 / 0.50)$
Maximum dispersal distance (D _{max})	0.5
Sex structure	Only-females
Simulations	1000 replications 50 years one time step = 1 year

Parameter	<i>M. glareolus</i>
Input maps	[nshr], [logha]
Habitat suitability (HS) function	[logha]
HS threshold	[logha] = 0.09
Neighborhood distance	1
Carrying capacity (K)	$(94/100) * 0.5 * (noc)$
Standard deviation of K	0.5
Initial abundance (N ₀)	$(12.3/100) * 0.5 * (noc)$
Maximum growth rate (R _{max})	1.71
Relative fecundity	$(8.84 - 0.51 * [nshr]) * 0.5 * 1.5$
Relative survival	$\exp(-4,4 - 1,11 * [logha]) / (\exp(-4,4 - 1,11 * [logha]) + 1)$
Density dependence	Scramble
Dispersal-distance function	$m_{ij} = 0.05 * \exp(-D_{ij}^1 / 0.36)$
Maximum dispersal distance (D _{max})	1.07
Sex structure	Only-females
Simulations	1000 replications 50 years one time step = 1 year

3.1.1. RAMAS Spatial Data program

Input maps. In order to spatially explicit the habitat requirements of the two investigated species, I created several GIS-generated maps. The Spatial Data program uses such map layers to identify the fragments in the landscape and to calculate the demographic parameters in each fragment. Based on the habitat requirements of the species I used to modeled some parameters (see the underlying sections **Habitat suitability (HS) function and HS threshold, Relative fecundity and Relative survival**), I created three map layers: 1) a map where, within each fragment, the cells have a value representing the fragment size in log-transformed hectares ($[\log ha]$), 2) a map where, within each fragment, the cells have a value representing the mean number of shrub individuals in 100 m^2 ($[nshr]$) and 3) a map where, within each fragment, the cells have a value representing the mean of the cover index of the fruit-bearing shrubs ($[absshr]$; Tab. 3.1). The resolution of the maps (width of each cell) is 10 m.

Habitat suitability (HS) function and HS threshold. The HS function is a function that links habitat characteristics to some measure of a habitat suitability. Therefore, is a quantitative relationship between physical and biological factors in the environment and the suitability of the habitat for a given species, not limited to any specific functional form or to any specific statistical procedure used to obtain the relationship.

The HS threshold is the minimum HS value (as defined by the HS

function) for the species modelled to reproduce. The definition assumes that the species can not reproduce in habitat that has a lower HS than this threshold, even though it can disperse or migrate through. In practice, to define this parameter means that the Spatial data subprogram, at the end of the calculations, identify a population only in those fragments having an HS value equal or greater respect to the threshold, leaving the other fragments empty.

In the present research I assumed that all the woodland fragments identified through the use of the software ArcView 3.3, using the Corine Land Cover as a main layer, were suitable habitat for both the investigated species. However, in order to obtain a realistic initial distribution of the two species in the landscape, i.e. not all the fragments are occupied at the beginning of the simulation process, I combined a HS function with a HS threshold.

Since both the survival and the fecundity of *M. avellanarius* showed to be strongly influenced by the structure of the shrub layer, I defined the HS function of that species only by the map layer [nshr], where, within each fragment, the cells have a value representing the mean number of shrub individuals in 100 m² of each fragment (Tab. 3.1). Since we characterized the vegetation structure only in 29 fragments of the 89 fragments present in the squared landscape, I randomly assigned the values of nshr estimated in the sampled fragments to the other not sampled fragments. Then, I defined as HS threshold the minimum value of nshr among the fragments where we

observed a reproductive event, i.e. 6.53 (Tab. 3.1).

Similarly to the previous species, for *M. glareolus* I defined the HS function by the map layer [logha], i.e. the log-transformed fragment size. Then, I defined as HS threshold the minimum value of logha among the fragments where we observed a reproductive event, i.e. 0.09 (Tab. 3.1).

Neighborhood distance. It represents the spatial scale at which the population can be assumed to be panmictic. It is used to find fragments in the HS map. Suitable cells (as defined by the HS threshold parameter) that are separated by a distance less than or equal to the neighborhood distance are regarded to be in the same fragment. Since the map resolutions are 10 m, for both species I adopted a neighborhood distance value of 1 (Tab. 3.1), i.e. all the cells spaced by 10 m or less belong to the same fragment.

Carrying capacity (K). The carrying capacity is a species-specific parameter which defines the capacity of the habitat (in terms of the availability of food, shelter and breeding resources) to hold up a given number of individuals (Bailey et al. 1984). In a logistic model of the population growth, the carrying capacity is the parameter which determines when density-dependent processes start to influence the population growth (Mills 2006).

In the present research I estimated the carrying capacity for both species in the following way. First, for each sampling session, I determined the greater value of densities among the investigated fragments (Appendix VI, Tab. 1 and Tab. 2). Second, I calculated the

mean of these values for all the sampling session. Then, I applied the following formula:

$$K = \frac{D_{max} \times F}{100} \times noc$$

where K is the carrying capacity, D_{max} is the mean among the greatest densities of each sampling session, F is the mean of the yearly female proportion (see the underlying section **Sex structure**), and noc is the number of cell composing each fragment. Since the RAMAS software works at a spatial scale of one cell (defined at 10 m^2 in the present research), and since the densities were estimated in hectares, I divided the product between the two means by 100 (Tab. 3.1).

RAMAS allows to modeling the environmental stochasticity by defining the **Standard deviation of K**. I estimated this parameter, for both species, as the standard deviation of the mean of the greater values of the densities of each sampling session (Tab. 3.1).

Initial abundance (N_0). This is the abundance value of a fragment at time t_0 , that is at the start of the simulation procedure. For both species, I calculated this parameter with the following formula:

$$N_0 = \frac{D_{first} \times F}{100} \times noc$$

where N_0 is the initial abundance, D_{first} is the mean among the fragment densities in the first sampling session of the year 2011, F is the mean of the yearly female proportion (see the underlying section **Sex structure**), and noc is the number of cell composing each fragment (Tab. 3.1; Appendix VI, Tab.1 and Tab. 2).

Maximum growth rate (Rmax). The maximum value of the population growth rate of a species, i.e. the maximum value of the ratios between the population size at time t and the population size at time $x+1$

t (Mills 2006), where x is a sampling session.

In the present research, I calculated, for both species, the yearly growth rate in each fragment in the following way: for each fragment, I divided the total number of individuals marked in a year by the total number of individuals marked in the previous year. Then, for each year I calculated the mean of the fragment growth rates. In order to avoid negative mean values (RAMAS GIS allows only positive values as input), I calculated the mean of only positive growth rates, and then used it as the maximum growth rate. Since for *M. avellanarius* I used the data of three sampling years, I obtained for each fragment two population growth rates; as a consequence, I first calculate, for each fragment, the

mean between the two growth rate, and than the mean among all fragments (Tab. 3.1).

Relative fecundity. In order to model this parameter I used, for both species, the averaged model resulted from my analysis on the species fertility (see Par. 2.2). Recent studies found that, in Central Italy forests, *M. avellanarius* females have often two breeding seasons per year (Panchetti & Carpaneto 2005). As a consequence, to account for this fact, and for the only one breeding season of the females of the year, I multiplied the fertility function of that species to 1.5 (Tab. 3.1). Similarly, I multiplied for the same factor the fertility function of *M. glareolus* (Oksanen et al. 2001).

Since I built only-females metapopulation models, the relative fecundity should be in terms of number of daughters per female. Therefore, I multiplied the fertility function by the mean of the yearly female proportion (Tab. 3.1). In Fig. 3.1 and Fig. 3.2 are graphed the relative fecundities of, respectively, *M. avellanarius* and *M. glareolus* of each fragment population as estimated by the Spatial Data program.

Relative survival. As in the case of the relative fecundity, I used, for both species, the averaged model resulted from my analysis on the species survival (see Par. 2.1). In Fig. 3.1 and Fig. 3.2 are graphed the relative survivals of, respectively, *M. avellanarius* and *M. glareolus* of each fragment population as estimated by the Spatial Data program.

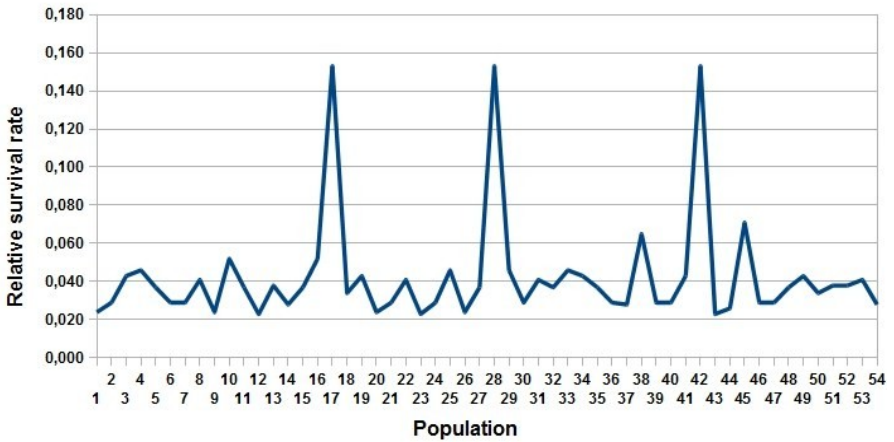
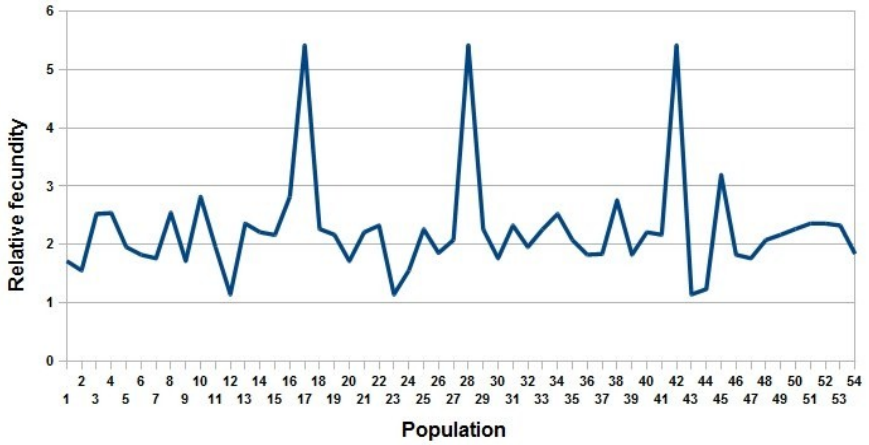


Figure 3.1. Estimates of relative fecundity (above) and relative survival (below) of *M. avellanarius* populations.

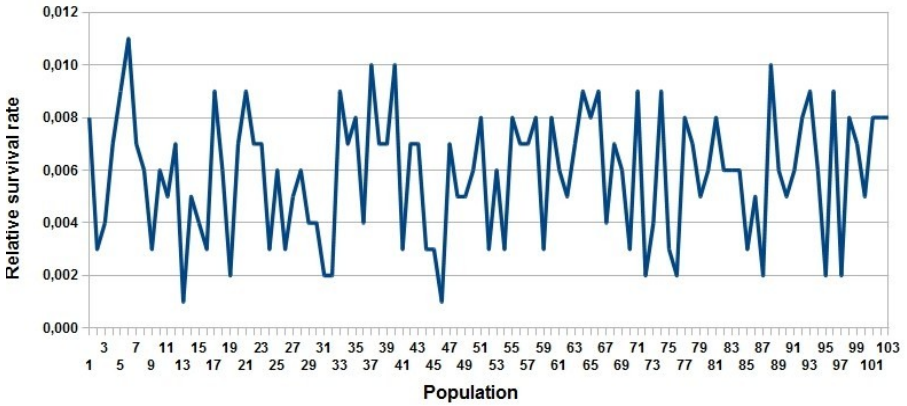
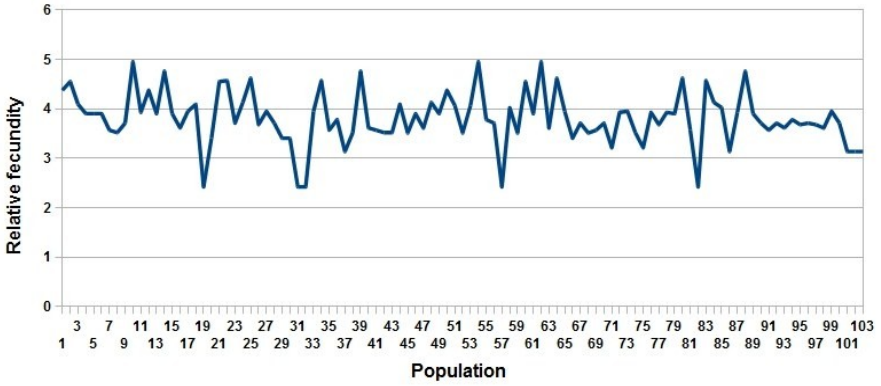


Figure 3.2. Estimates of relative fecundity (above) and relative survival (below) of *M. glareolus* populations.

Distances. When the Spatial Data program creates the HS map, it build a matrix of the distances between all pairs of fragments. The program allows the choise among three types of distances: edge to edge, center to edge and center to center. Since the distance between the center of each fragment and its edges might be considered irrelevant respect to the distance between the same fragment and the neighborhoods, I choose the edge to edge option.

Density dependence. Density dependence is a relationship that describes the growth of a population as a function of its density or abundance. Population with abundant resources (compared to the number of individuals in the population) can grow exponentially for a period of time. As population size increases, it must approach a point at which there are more individuals than can be supported by the available resources. The effect of limited resources results in some kind of feedback that limits the population growth. RAMAS allows to model three types of density-dependence: scramble competition, contest competition and ceiling model. In the scramble type resources are presumed to be shared more-or-less equally among the individuals, while in the contest and in the ceiling type some individuals receive more resources at the expense of other individuals. On the base of the biology of the two investigated species, I adopt for both the scramble competition density-dependence (Tab. 3.1).

Dispersal. For a metapopulation to persist longer than each of its populations, the extinct populations (i.e. the empty fragments) must have a chance to be recolonized by individuals dispersing from extant

populations. Therefore we can expect that in most cases dispersal among local populations will decrease the extinction risk of a species.

In RAMAS the dispersal is defined as the movement of individuals from one population to another. Dispersal rate is specified as the proportion (not as the total number) of dispersing individuals per time step from one (source) population to another (target). In RAMAS the dispersal is modeled by the following **dispersal-distance function**:

$$m_{ij} = a \times \exp\left(\frac{D_{ij}^c}{b}\right)$$

where m_{ij} is the dispersal rate between the fragment i and the fragment j , a is the proportion of individuals that from a source population arrive to a target population, b is the decrease in the dispersal rate as a function of the distance between the source and the target fragments, D_{ij} is the distance between the source and the target fragments, c is a constant which determines the shape of the function (e.g. if $c = 1$ then the function becomes a negative exponential function). Moreover, the program needs that also a maximum dispersal distance, D_{max} , has specified.

Due to several limits in the present research, I approached the parameterization of the dispersal in the following ways. For *M. avellanarius*, since we did not recorded any migration of marked

individuals from a fragment to another, I arbitrarily assume $a = 0.01$ (i.e. one individual every 100 individuals of a source population arrive to a target population). I set $b = 0.5$, since 0.5 km was the maximum distance of the a fragment where we recorded a colonization event from the nearest fragment with an occupancy probability greater than 0.5, $c = 1$ to reflect a negative exponential shape of the dispersal function, and $D_{max} = 1$ km; the distance of 1 km is the greater distance traveled by the species reported in previous researches (Bright & Morris 1992, Juškaitis 1997, 2008; Fig. 3.3).

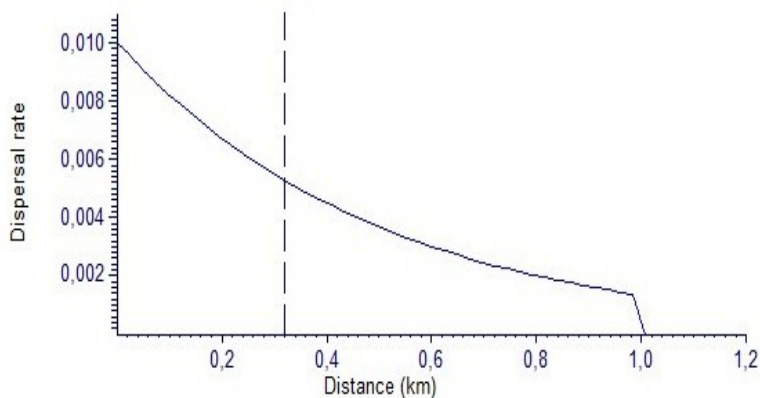


Figure 3.3. Shape of the dispersal-distance function of *M. avellanarius*.

During the two years of *M. glareolus* sampling, we recorded 14 migration events of marked individuals from a fragment to another (Tab. 3.2). Therefore, I based the parameterization of the dispersal function for that species on such data. I calculated: i) the maximum edge-to-edge distance between two fragments where we detected a migration, 1.07 km; ii) the mean – in km – of the edge-to-edge distances between the pairs of fragments where migrations events were detected, 0.36 km; iii) the mean, among the fragments from where individuals migrated, of the proportion of migrated individuals respect to the mean abundance between the session when the migrated individuals were marked and the session when they were recaptured in the destination fragment, 0.05. Therefore, I setted: $a = 0.05$, $b = 0.36$, $c = 1$ (to reflect a negative exponential shape of the dispersal function) and $D_{max} = 1.07$ (Tab. 3.1; Fig. 3.4).

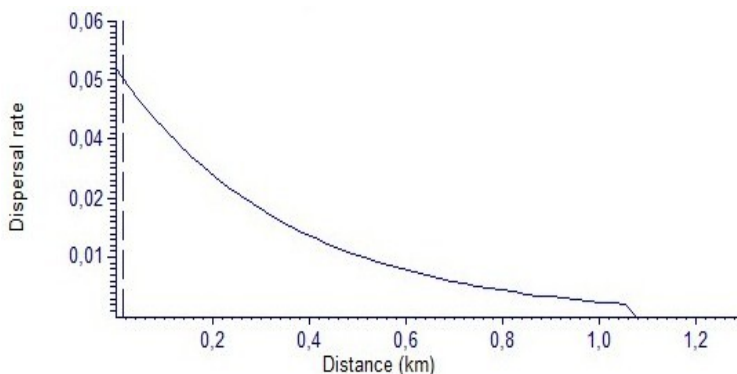


Figure 3.4. Shape of the dispersal-distance function of *M. glareolus*.

Table 3.2. Migration events (fragment-to-fragment movements) of *M. glareolus* recorded during the two years of sampling. The table reports the edge-to-edge distances, in meters, between each pair of fragments, and the proportion, respect to the source-fragment population size, of migrating individuals.

Fragment OUT	Fragment IN	Distance (m)
MG15	MG17	50,3
MG17	MG15	50,3
MG16	MG14	117,1
MG20	MG21	181,1
MG20	MG21	181,1
MG20	MG21	181,1
MG20	MG21	181,1
MG21	MG20	181,1
MG21	MG20	181,1
MG21	MG20	181,1
MG6	MG20	639,5
MG1	MG12	800,9
MG21	MG19	1072,4
MG19	MG20	1072,4

In Fig. 3.5 and Fig. 3.6 are showed the HS maps with the identified populations of, respectively, *M. avellanarius* (54 populations) and *M. glareolus* (103 populations). In Tab. 3.3 and Tab. 3.4 are reported, respectively for *M. avellanarius* and *M. glareolus*, the

estimated carrying capacity, initial abundance and relative vital rates of each population.

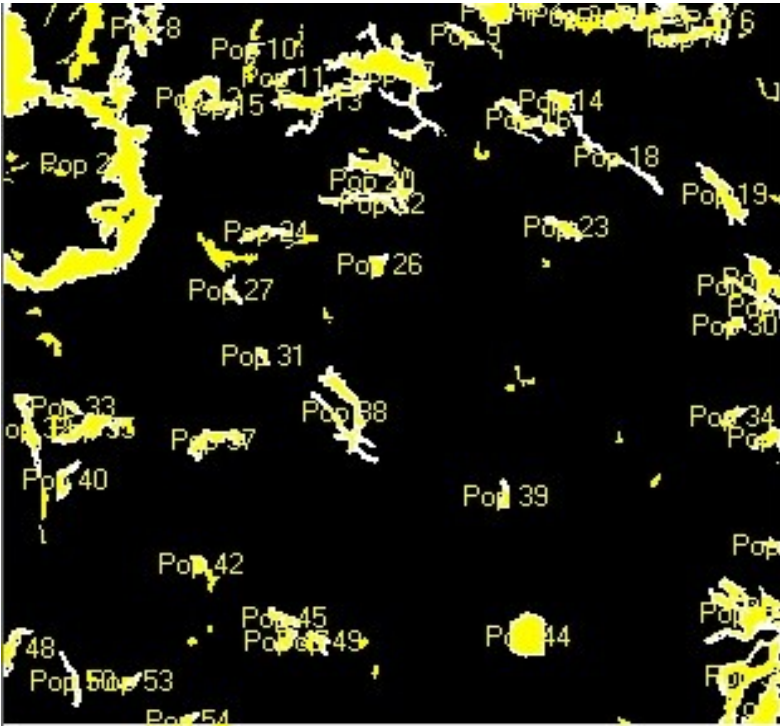


Figure 3.5. Habitat suitability map of *M. avellanarius* metapopulation. The yellow polygons represents the woodland fragments. 54 fragments out to the 103 within the squared landscape are occupied by a population.

Table 3.3. Estimates of the carrying capacity (K), th initial abundance (N_0) and the relative vital rates of each identified population of *M. avellanarius*.

Population	K	N_0	Rel. fecundity	Rel. survival	Population	K	N_0	Rel. fecundity	Rel. survival
1	6	4	1,72	0,024	28	1	1	5,42	0,153
2	1	1	1,56	0,029	29	2	1	2,26	0,046
3	1	1	2,53	0,043	30	2	1	1,76	0,029
4	2	1	2,54	0,046	31	1	1	2,33	0,041
5	9	5	1,96	0,037	32	7	4	1,96	0,037
6	3	2	1,83	0,029	33	1	1	2,26	0,046
7	5	3	1,76	0,029	34	2	1	2,53	0,043
8	8	5	2,55	0,041	35	8	5	2,08	0,037
9	2	1	1,72	0,024	36	3	2	1,83	0,029
10	1	1	2,82	0,052	37	6	4	1,84	0,028
11	1	1	1,96	0,037	38	13	8	2,76	0,065
12	8	5	1,14	0,023	39	2	1	1,83	0,029
13	12	7	2,36	0,038	40	3	2	2,21	0,029
14	3	2	2,21	0,028	41	1	1	2,17	0,043
15	2	1	2,17	0,037	42	2	1	5,42	0,153
16	6	3	2,82	0,052	43	2	1	1,14	0,023
17	28	16	5,42	0,153	44	13	8	1,24	0,026
18	5	3	2,27	0,034	45	3	2	3,2	0,071
19	8	5	2,17	0,043	46	16	9	1,83	0,029
20	10	6	1,72	0,024	47	2	1	1,76	0,029
21	128	75	2,21	0,029	48	4	2	2,08	0,037
22	2	1	2,33	0,041	49	2	1	2,17	0,043
23	3	2	1,14	0,023	50	2	1	2,27	0,034
24	3	2	1,56	0,029	51	17	10	2,36	0,038
25	8	5	2,26	0,046	52	10	6	2,36	0,038
26	2	1	1,86	0,024	53	1	1	2,33	0,041
27	1	1	2,08	0,037	54	1	1	1,84	0,028

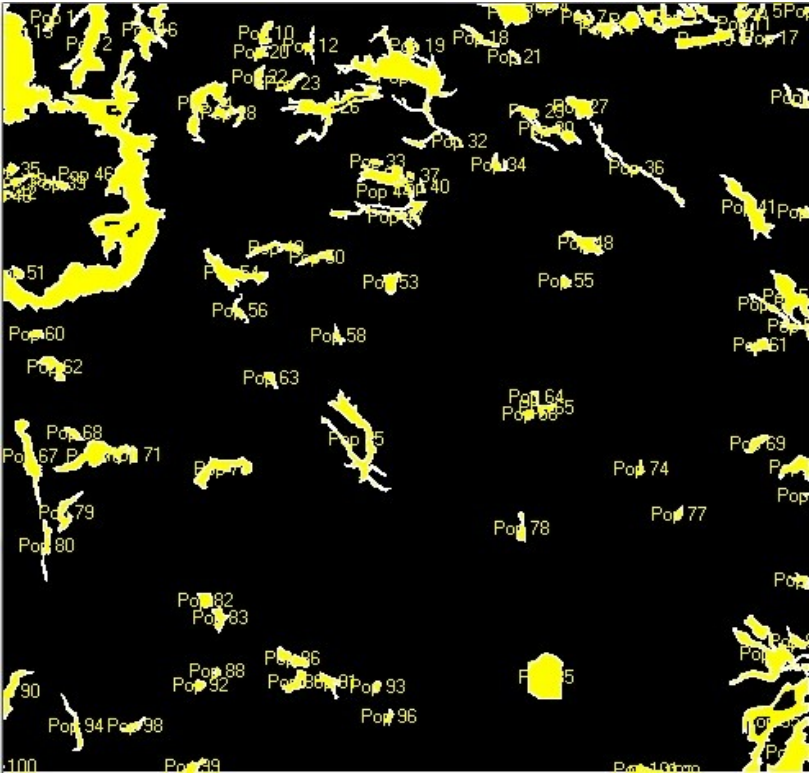


Figure 3.6. Habitat suitability map of *M. glareolus* metapopulation. The yellow polygons represents the woodland fragments. All the 103 fragments within the squared landscape are occupied by a population.

Table 3.4. Estimates of the carrying capacity (K), the initial abundance (N_0) and the relative vital rates of each identified population of *M. glareolus*.

Population	K	N_0	Rel. fecundity	Rel. survival	Population	K	N_0	Rel. fecundity	Rel. survival
1	63	8	4,38	0,008	53	180	23	4,07	0,006
2	1159	152	4,55	0,003	54	602	79	4,96	0,003
3	480	63	4,09	0,004	55	57	7	3,78	0,008
4	86	11	3,9	0,007	56	109	14	3,71	0,007
5	37	5	3,9	0,009	57	101	13	2,42	0,007
6	13	2	3,9	0,011	58	62	8	4,03	0,008
7	106	14	3,57	0,007	59	160	21	3,51	0,003
8	178	23	3,52	0,006	60	71	9	4,55	0,008
9	674	88	3,71	0,003	61	136	18	3,9	0,006
10	131	17	4,96	0,006	62	212	28	4,96	0,005
11	222	29	3,93	0,005	63	83	11	3,61	0,007
12	98	13	4,38	0,007	64	39	5	4,62	0,009
13	8	1	3,9	0,001	65	68	9	3,95	0,008
14	205	27	4,76	0,005	66	52	7	3,41	0,009
15	376	49	3,9	0,004	67	548	72	3,71	0,004
16	644	84	3,62	0,003	68	88	12	3,51	0,007
17	44	6	3,95	0,009	69	133	17	3,57	0,006
18	156	20	4,09	0,006	70	662	87	3,71	0,003
19	13	2	2,42	0,002	71	52	7	3,21	0,009
20	89	12	3,41	0,007	72	259	34	3,93	0,002
21	47	6	4,55	0,009	73	501	65	3,95	0,004
22	100	13	4,57	0,007	74	36	5	3,52	0,009
23	87	11	3,71	0,007	75	1046	137	3,21	0,003
24	609	80	4,13	0,003	76	10	1	3,93	0,002
25	136	18	4,62	0,006	77	55	7	3,68	0,008
26	932	122	3,68	0,003	78	119	16	3,93	0,007
27	271	35	3,95	0,005	79	239	31	3,9	0,005
28	194	25	3,71	0,006	80	194	25	4,62	0,006
29	1	0	3,41	0,004	81	82	11	3,57	0,008
30	452	59	3,41	0,004	82	130	17	2,42	0,006
31	2206	289	2,42	0,002	83	146	19	4,57	0,006
32	21	3	2,42	0,002	84	127	17	4,13	0,006
33	40	5	3,95	0,009	85	1016	133	4,03	0,003
34	106	14	4,57	0,007	86	223	29	3,14	0,005
35	64	8	3,57	0,008	87	1240	162	3,93	0,002
36	372	49	3,78	0,004	88	27	4	4,76	0,010
37	27	4	3,14	0,010	89	166	22	3,9	0,006
38	64	8	3,52	0,007	90	307	40	3,71	0,005
39	93	12	4,76	0,007	91	142	19	3,57	0,006
40	30	4	3,62	0,010	92	57	8	3,71	0,008
41	642	84	3,57	0,003	93	49	6	3,62	0,009
42	19	3	3,52	0,007	94	188	25	3,78	0,006
43	1	0	3,52	0,007	95	1355	177	3,68	0,002
44	815	107	4,09	0,003	96	48	6	3,71	0,009
45	65	8	3,51	0,003	97	821	107	3,68	0,002
46	10061	1316	3,9	0,001	98	80	11	3,61	0,008
47	126	17	3,61	0,007	99	115	15	3,95	0,007
48	271	35	4,13	0,005	100	1	0	3,71	0,005
49	205	27	3,9	0,005	101	52	7	3,14	0,008
50	135	18	4,38	0,006	102	5	1	3,14	0,008
51	74	10	4,07	0,008	103	2	0	3,14	0,008
52	618	81	3,51	0,003					

3.1.2. RAMAS Metapopulation Model program

Sex structure. As abovementioned I built only-females metapopulation models for both species (Tab. 3.1). As a consequence, I multiplied the carrying capacities, the initial abundances and the relative fecundities by the means of the yearly female proportions.

Stochasticity. Fluctuation is an obvious and often predominant feature of population dynamics, and any realistic attempt to model those dynamics must account for this fact. RAMAS allows to build stochastic models of population dynamics by incorporating both environmental fluctuations and demographic variability. In order to account for those two types of variability: i) I checked the **Demographic stochasticity** option, ii) in order to incorporate the environmental stochasticity, I setted the parameter **Standard deviation of K** as the standard deviation of the mean of the greater values of the densities of each sampling session (Tab. 3.1).

Simulation. In each simulation I carried out: i) I setted 1000 replications, ii) the duration was 50 years, iii) one time step correspond to one year.

3.2. RAMAS population viability analysis

RAMAS Metapopulation Model uses several different ways of summarizing the results of a population viability analysis. Some of these are traditional measures such as expected number of individuals in the

future or expected occupancy rate in a metapopulation. However, the majority of the measures used to express PVA results are risk-related. Risk is the probability of an unwanted event (such as extinction or population decline). Population-level risk analysis attempts to assess the likelihood of a population or species extinction or decline by some specified time in the future under various natural conditions and scenarios of management.

Below, I list and define the RAMAS measures I used to express the results of the PVAs I carried out to predict the persistence of *M. avellanarius* and *M. glareolus* metapopulations in the landscape under investigation.

Metapopulation occupancy. It is a summary of the occupancy of the metapopulation as it changes through time. It shows the change in the number of extant populations (i.e. occupied fragments) through time.

Interval risk percentage of decline. It is the risk of a percentage population declining by a given amount from the initial population at least once before the end of the simulated time period (50 years in the present research).

Expected minimum abundance. It is the average (over all replications) of the minimum metapopulation abundance of the trajectory. It is an estimate of the smallest metapopulation size that is expected to occur within the simulated time period (50 years in the present research).

Ramas Metapopulation Model plots all risk curves together with 95% confidence intervals based on Kolmogorov-Smirnov test statistic

(Sokal & Rohlf 1981). The width of the confidence interval is exclusively a function of the number of replication. With 1000 replications, the risk curves have 95% confidence limits of about +/- 0.03 of +/- 3%.

In the next two section I will present the results of the PVAs on *M. avellanarius* and *M. glareolus* metapopulations.

M. avellanarius

At the beginning of the simulated period, RAMAS estimated a mean metapopulation abundance (sum of the abundances of all populations) of 237 individuals (Fig. 3.7). The temporal trend of this value is a decrease until it reaches a mean value of 160 individuals at the end of the 50 years.

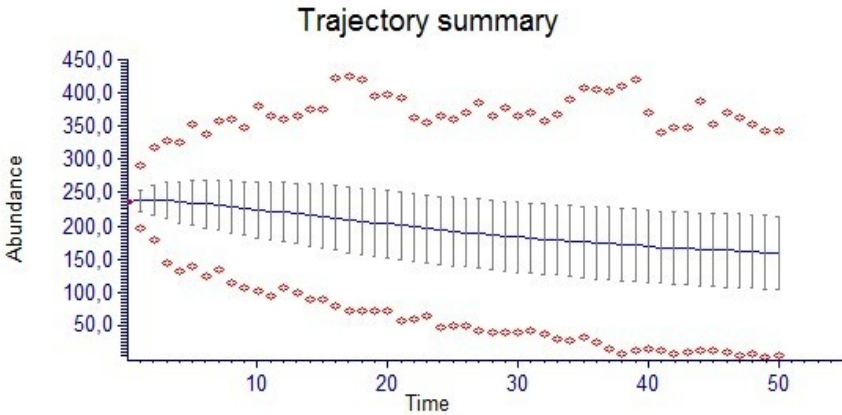


Figure 3.7. Temporal trend of the abundance of *M. avellanarius* metapopulation (total number of individuals) in the 50-year period simulated. Vertical lines represent 95% confidence interval at each time step (one year); circles represent, at each time step, the maximum (upper circle) and the minimum (lower circle) abundances resulted from the 1000 replicates.

Of the 54 fragments occupied at the beginning of the simulated period, only a mean of 6 fragments resulted occupied at the end of the 50-year period simulated (Fig. 3.8). Following an early rapid decline in the metapopulation occupancy (after ten years in 35 out of 54 fragments occupied at the beginning of the simulation a local extinction occurred), the loss of populations slows down, although it does not stop (Fig. 3.8).

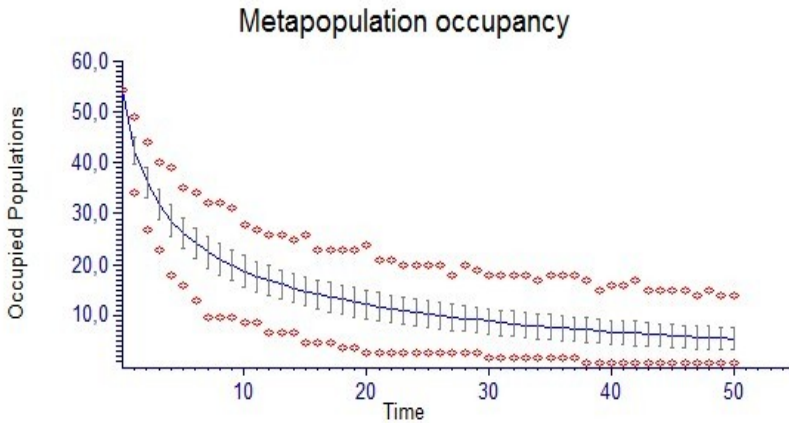


Figure 3.8. Temporal trend of the occupancy of *M. avellanarius* metapopulation in the 50-year period simulated. Vertical lines represent 95% confidence interval at each time step (one year); circles represent, at each time step, the maximum (upper circle) and the minimum (lower circle) number of fragments occupied resulted from the 1000 replicates.

As showed in Fig. 3.9, the probability of a decline in the metapopulation abundance is very high for low percentages of decline (e.g. a decline of about 10-20% have a probability of about 0.99-0.93), relatively high for medium percentages of decline (e.g. a decline of

about 40-50% have a probability of about 0.63-0.4), and low for high percentages of decline (e.g. a decline of about 70-80% have a probability of about 0.08-0.02).

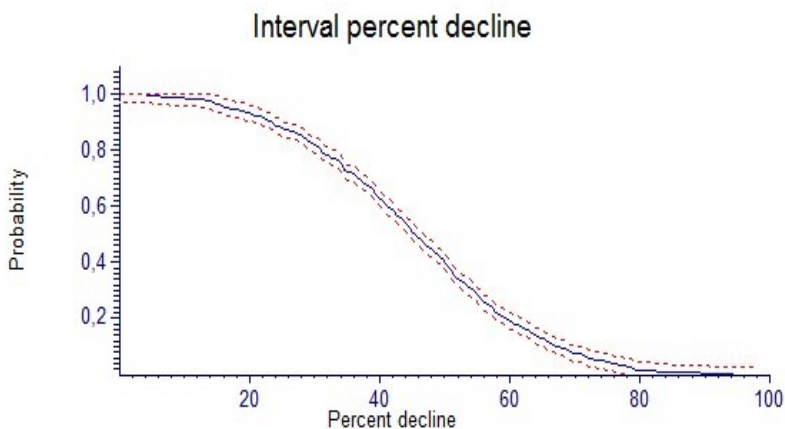


Figure 3.9. Probability of a percentage decline from the initial *M. avellanarius* metapopulation size (total number of individuals) at least once before the end of the 50-year period simulated. Dotted lines represent 95% confidence intervals.

M. glareolus

At the beginning of the simulated period, RAMAS estimated a mean metapopulation abundance (sum of the abundances of all populations) of 4701 individuals (Fig. 3.10). During the first 10 years of the simulated period, the abundance values showed a rapid and exponential increase (at the 10-years time step the metapopulation abundance is about 29000 individuals). At the end of the 50-years simulated period the predicted metapopulation abundance is 30339 individuals, more then six times the initial value.

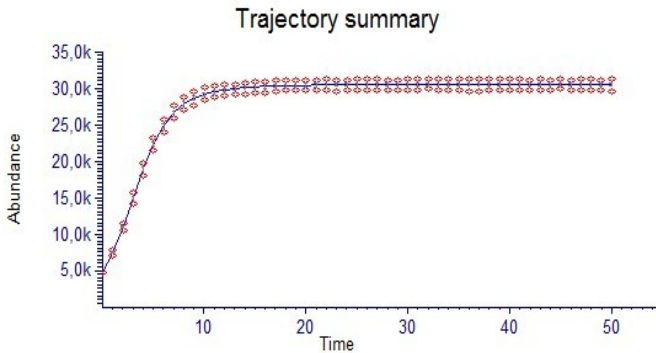


Figure 3.10. Temporal trend of the abundance of *M. glareolus* metapopulation (total number of individuals) in the 50-year period simulated. Vertical lines represent 95% confidence interval at each time step (one year); circles represent, at each time step, the maximum (upper circle) and the minimum (lower circle) abundances resulted from the 1000 replicates.

The simulation results showed that the spatial distribution of *M. glareolus* populations (i.e. the metapopulation occupancy) remain constant through the entire simulated period (Fig. 3.11). As a result of the predicted metapopulation abundance and occupancy, the probability of a metapopulation decline is 0 during the entire 50-year simulated period (Fig. 3.12).

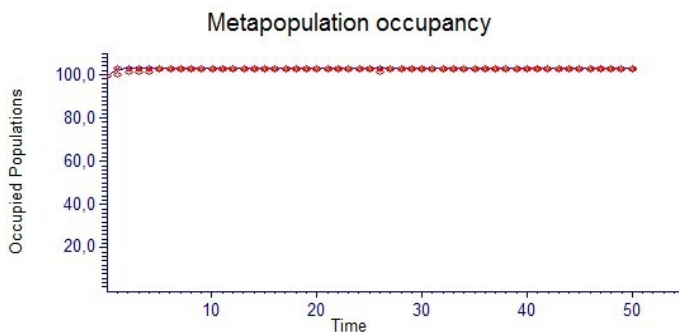


Figure 3.11. Temporal trend of the occupancy of *M. glareolus* metapopulation in the 50-year period simulated. Vertical lines represent 95% confidence interval at each time step (one year); circles represent, at each time step, the maximum (upper circle) and the minimum (lower circle) number of fragments occupied resulted from the 1000 replicates.

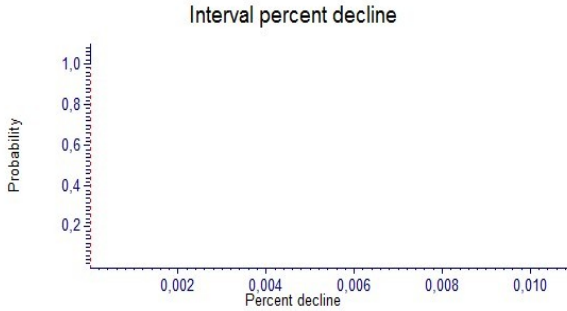


Figure 3.12. Probability of a percentage decline from the initial *M. glareolus* metapopulation size (total number of individuals) at least once before the end of the 50-year period simulated.

3.3. Simulation protocols and optimal conservation strategies

The PVA of the spatially structured population of *M. avellanarius* showed a negative trend during the simulated period both in the occupancy pattern and in the total abundance of individuals. On the contrary, the projection of *M. glareolus* populations showed how the species, through the simulated 50-years period, will maintain the initial

occupancy pattern, with all the forest fragments being occupied, while the average abundance will increase more than six folds.

Following these results, and those on the analysis of the demographic parameters, I developed a simulation protocol only for *M. avellanarius*, in order to simulate the population responses, in terms of viability, to different landscape management scenarios. All simulated conservation scenarios were constrained by a fixed financial budget of 1 million of euros.

In the following sections I will expone the optimization procedure.

M. avellanarius

The 50-year projection of the metapopulation persistence of that species predicted a dramatic loss of occupied fragments and a relatively high probability of important percentage declines in the metapopulation abundance (Par. 3.2). From the demographic analysis (Par. 2.2.1), resulted that both vital rates, survival and fertility, are positively influenced by a complex shrub layer (i.e. more fruit-bearing shrub individuals and more fruit-bearing shrub cover means higher survival probability and higher mean litter size). Therefore, I developed a simulation protocol for each of the following two conservation strategies.

- Habitat restoration: the purchase of a defined amount of non-habitat land and its conversion in habitat.
- Habitat quality improvement: the enrichment of the shrub

layer within the forest stands through plantation of a defined number of fruit-bearing shrub individuals.

For each conservation strategy, I ranked the simulated landscape scenarios starting from the one that, at the end of the simulated period, present the highest metapopulation abundance and lowest probabilities of percentage of decline. These two first ranked landscape scenarios were then compared in order to determine the most cost-effective conservation strategy.

Conservation budget and costs. In the present research I adopted an optimization approach in which the implementation of each abovementioned conservation action were constrained by the availability of a fixed amount of financial funds. In order to approach a realistic decision-making procedure I fixed the available funds at 1 million of euros, that is the maximal amount of funding given by the LIFE Programm of the European Commission in supporting environmental and nature conservation projects (<http://ec.europa.eu/environment/life/>).

In order to determine the cost-effectiveness of the two strategies, I collected the data on the economic value of:

- the terrains of arable and pasture land uses: 8000 € (data source: Income Revenue Authority – Mean Rural Values of the Province of Viterbo, 2013; http://www.agenziaentrate.gov.it/mt/Osservatorio%20immobiliare/valori_agricoli_medi/lazio/VT_2013.pdf);

- the afforestation process per hectare: 12000 € (data source LIFE project LIFE09 NAT/IT 000093 “ECO-RICE”, personal communication of Dr. Luca Cristaldi);
- a single fruit-bearing shrub individual and its plantation: 17,80 € (data source: Piedmont Region – Price List of Public Works 2013, <http://www.regione.piemonte.it/oopp/prezzario/index13.htm>; Sicily Region – Price List of Public Works 2013, http://pti.regione.sicilia.it/portal/page/portal/PIR_PORTALE/PIR_LaStrutturaRegionale/PIR_AssInfrastruttureMobilita/PIR_InfrastruttureMobilitaTrasporti/PIR_PrezzarioLavoriPubblici).

By dividing the available budget to the cost of each conservation strategy unit (e.g. one hectare of broadleaved woodland in the habitat preservation scenario), I determined the amount of purchasable resources for each type of conservation strategy:

- habitat restoration: the afforestation of 50 hectares of terrain of arable and/or pasture land uses;
- habitat quality improvement: the plantation of 56180 fruit-bearing shrub individuals.

Simulation protocols. For each conservation strategy I will expose the elaboration of the simulation protocol, the analysis and results of the spatially explicit PVAs carried out for each landscape scenarios. The SEPMS of each simulation were parameterized with the

same parameters reported in Tab. 3.1.

Habitat restoration. In this conservation scenario I assumed that the total amount of the budget is invested in purchasing 50 hectares of arable and pasture land use terrains for woodland restoration. I simulated three landscape scenarios.

- In the first scenario the afforestation of 50 hectares was carried out in only one fragment (Fig. 3.13).
- In the second scenario the afforestation was carried out in two fragment 25 hectares sized (Fig. 3.14).
- In the third scenario the afforestation was carried out in five fragment 10 hectares sized (Fig 3.15).

Except to the fragment size, the created fragments do not have the data needed to fit the SEPMs, i.e. the cell values of the map layer [nshr] and [abshr]. Therefore, I assigned them: to [nshr] the mean value of the nshr covariate; to [abshr] the mean value of the abshr covariate.

For each landscape scenario I replicated the simulation in four different habitat configurations, i.e. different geographical positions of the restored fragment, in order to look for significant differences in PVAs results due to the landscape configuration (Appendix V). The PVAs showed identical results for all landscape scenarios. As a consequence, I compared the results of one replicate for each landscape scenario.

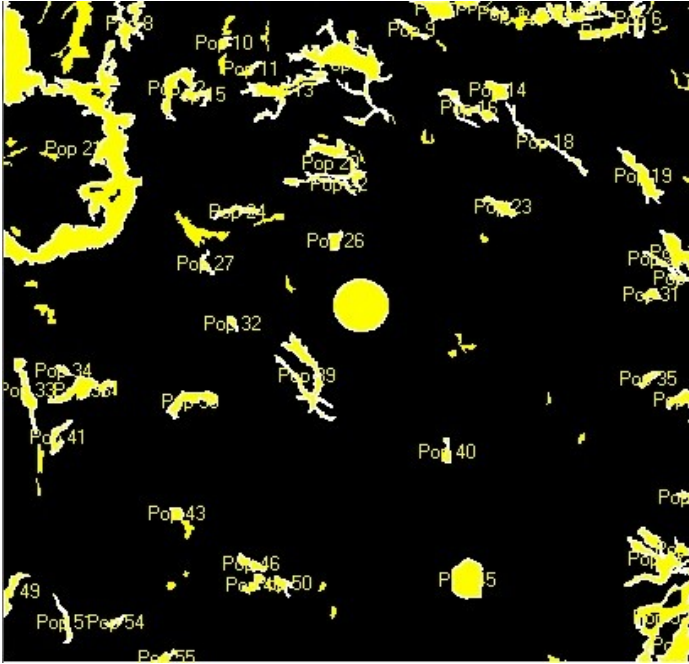


Figure 3.13. Habitat suitability map of *M. avellanarius* for one simulation of the restorations of 50 hectares of habitat in one fragment (the yellow circle). The yellow polygons represents the woodland fragments. 55 fragments out to the 103 within the landscape are occupied by a population.

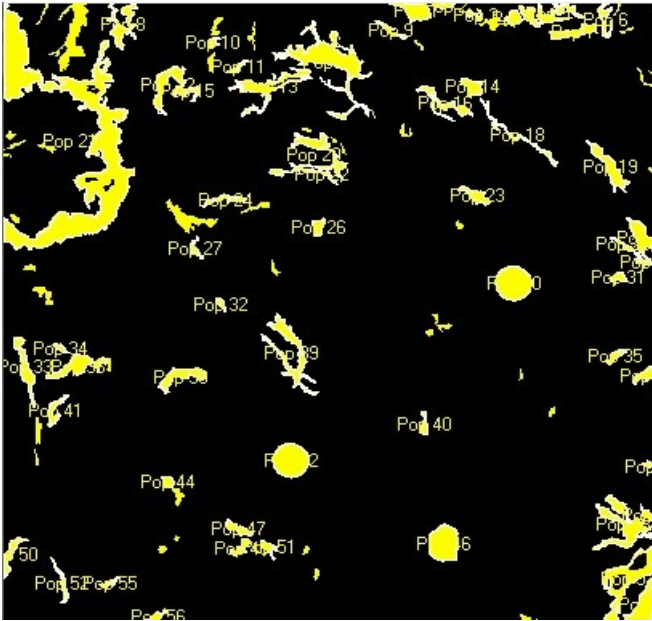


Figure 3.14. Habitat suitability map of *M. avellanarius* for one simulation of the restorations of 50 hectares of habitat in two fragments 25 hectares sized (the two yellow circles). The yellow polygons represents the woodland fragments. 56 fragments out to the 103 within the squared landscape are occupied by a population.

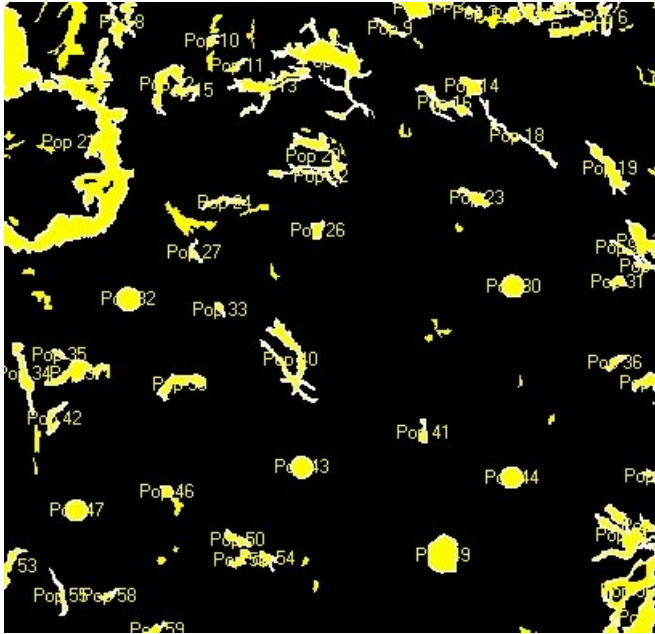


Figure 3.15. Habitat suitability map of *M. avellanarius* for one simulation of the restorations of 50 hectares of habitat in five fragments 10 hectares sized (the five yellow circles). The yellow polygons represents the woodland fragments. 59 fragments out to the 103 within the squared landscape are occupied by a population.

The 50-year projections of species viability showed that the most cost-effective solution is the one where the 50 hectares were afforested in only one fragment: in fact, this solution presented the highest

metapopulation abundance (174 individuals) at the end of the simulated period (Fig. 3.16), and the lower probabilities of percentage declines (Fig. 3.17).

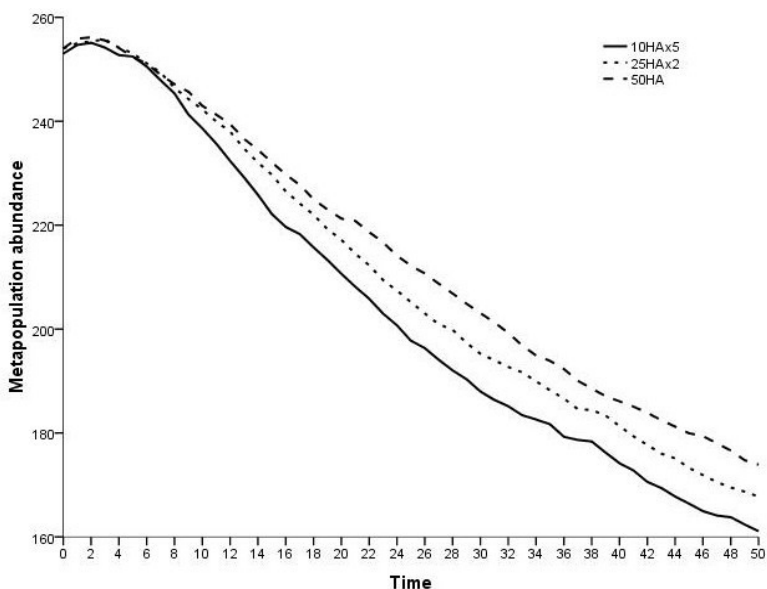


Figure 3.16. Comparison of the results of the metapopulation abundances predicted by the PVAs on the three landscape scenarios of habitat restoration. 10HAx5 = restoration of five fragments 10 hectares sized; 25HAx2 = restoration of two fragments 25 hectares sized; 50HA = restoration of one fragments 50 hectares sized.

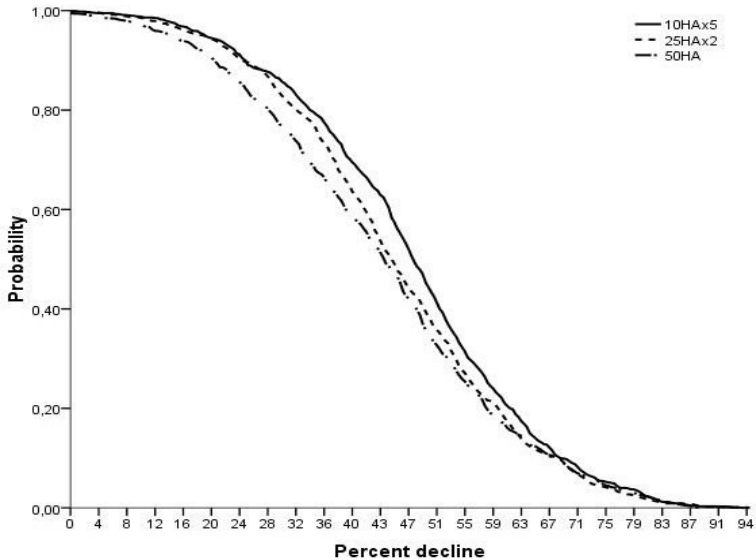


Figure 3.17. Comparison of the results of the probability of percentages decline predicted by the PVAs on the five landscape scenarios of habitat preservation. 10HAx5 = restoration of five fragments 10 hectares sized; 25HAx2 = restoration of two fragments 25 hectares sized; 50HA = restoration of one fragments 50 hectares sized.

Habitat quality improvement. In this conservation scenario I assumed that the total amount of the budget is used to purchase 56180 fruit-bearing shrub individuals and to to plant them in defined

fragments. I based this conservation strategy on the manipulation of the two parameters describing the shrub layer complexity, i.e. the mean number of fruit-bearing shrub individuals per 100 m² (nshr), and the index of fruit-bearing shrub cover (abshr; Tab. 3.1), because an increase in those parameters showed to positively influence the species vital rates (Par. 2.2.1).

I elaborated four landscape scenarios where different allocation of the total amount of shrub individuals were simulated.

- In the first landscape scenario (Fig. 3.18), an equal number of shrub individuals were allocated in each 0.01 ha of habitat. Since the residual habitat in the landscape is 762 ha, I added 0.74 to each fragment value of nshr. Increasing nshr means proportionally increasing also abshr. Therefore, I multiplied each fragment value of abshr by a scaling factor of 1.40, that is the mean of the nshr:abshr ratio.
- In the second landscape scenario (Fig. 3.19), I allocated the total amount of shrub individuals to the fragments with higher nshr values, in order to maximize thier quality. Starting from the fragment with the highest value I added shrub individuals until the maximum value of nshr (i.e. the higher nshr value among the sampled fragments, 11; Appendix I, Tab. 3) was reached. Then, I proceeded in the same way with the fragment with the second higher value of nshr, and so on until the total amount of fruit-bearing shrub individuals for habitat quality improvement was allocated. In

order to proportionally increase abshr, I assigned the maximum value of abshr (i.e. the higher abshr value among the sampled fragments, 15.9; Appendix I, Tab. 3) to the manipulated fragments. A total of 30 fragments were manipulated.

- In the third landscape scenario (Fig. 3.20), I allocated the total amount of shrub individuals to the largest fragment. Since the size of that fragment is 214,11 ha (Appendix I, Tab. 1), I added 2.62 to the fragment value of nshr. As in the first landscape scenario, in order to proportionally increase abshr I multiplied the fragment value of abshr by the scaling factor of 1.40.
- In the fourth landscape scenario (Fig. 3.21), I allocated the total amount of shrub individuals to the smaller fragments. Starting from the smallest fragment, I added shrub individuals until the maximum value of nshr (i.e. the higher nshr value among the sampled fragments, 11; Appendix I, Tab. 3) was reached. Then, I proceeded in the same way with the second smallest fragment value, and so on until the total amount of fruit-bearing shrub individuals for habitat quality improvement was allocated. As in the second landscape scenario, I assigned the maximum value of abshr (i.e. the higher abshr value among the sampled fragments, 15.9; Appendix I, Tab. 3) to the manipulated fragments. A total of 62 fragments were manipulated.

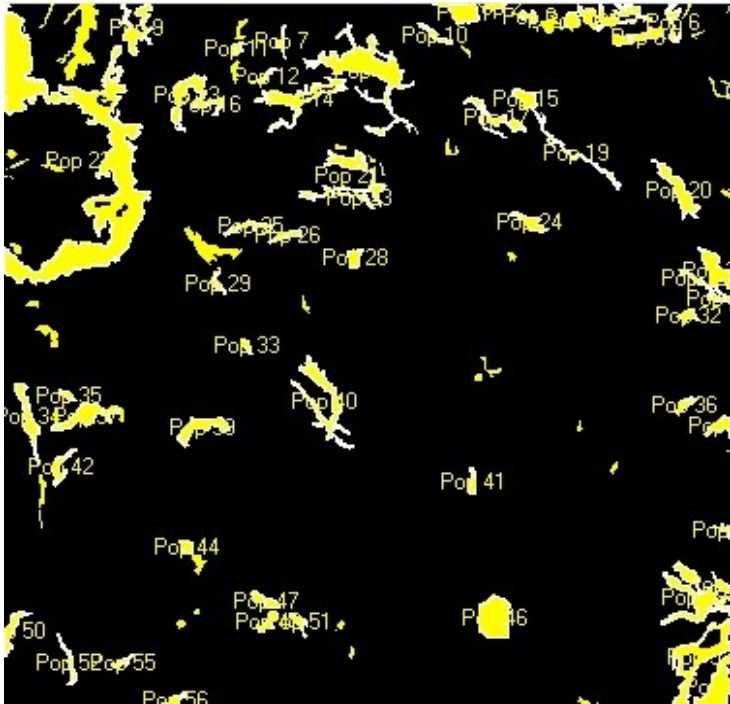


Figure 3.18. Habitat suitability map of *M. avellanarius* for the habitat quality improvement strategy. This landscape scenario assumed that the total amount of fruit-bearing shrub individuals were equally allocated on each 100 m² of habitat (see text for more details). The yellow polygons represents the woodland fragments. 56 fragments out to the 103 within the squared landscape are occupied by a population.

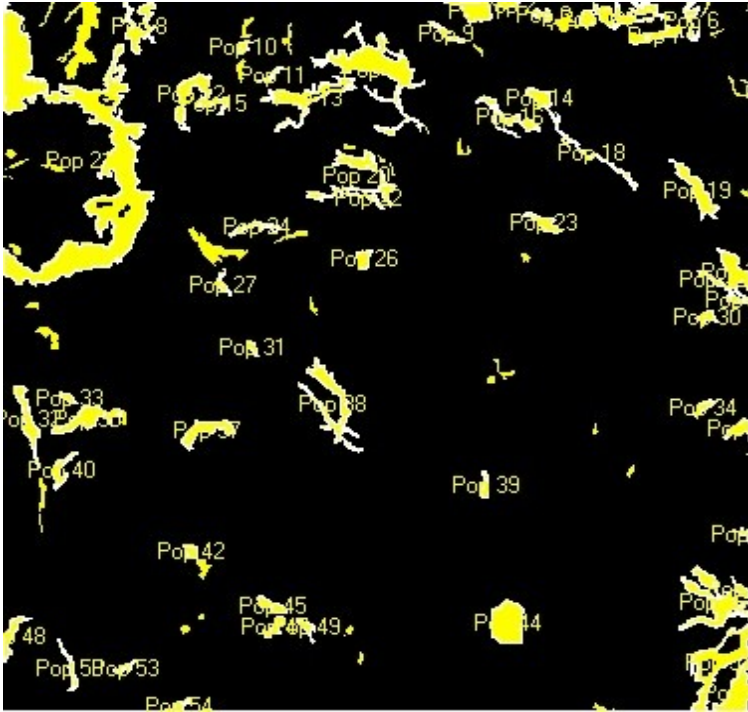


Figure 3.19. Habitat suitability map of *M. avellanarius* for the habitat quality improvement strategy. This landscape scenario assumed that the total amount of fruit-bearing shrub individuals were allocated to the fragments with higher *nshr* values (see text for more details). The yellow polygons represents the woodland fragments. 54 fragments out to the 103 within the squared landscape are occupied by a population.

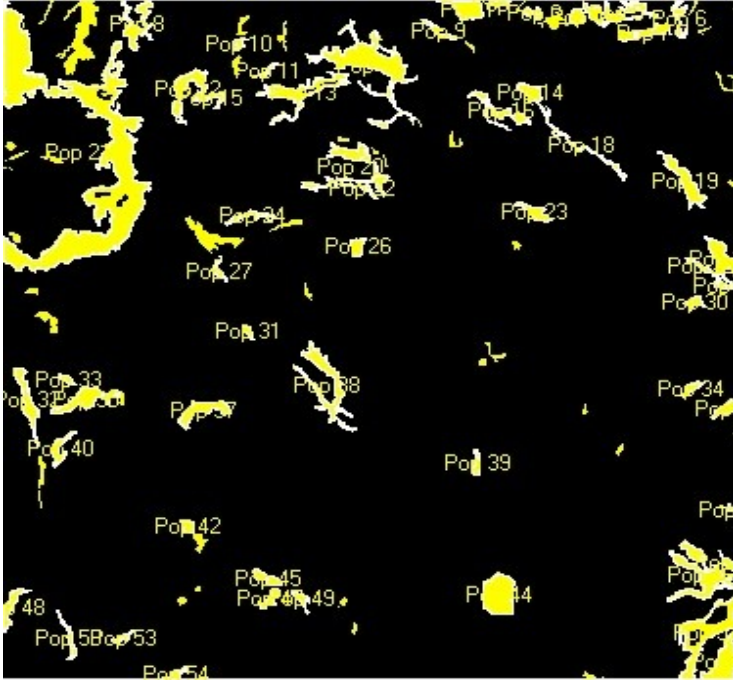


Figure 3.20. Habitat suitability map of *M. avellanarius* for the habitat quality improvement strategy. This landscape scenario assumed that the total amount of fruit-bearing shrub individuals were allocated to the greatest fragment (see text for more details). The yellow polygons represents the woodland fragments. 54 fragments out to the 103 within the squared landscape are occupied by a population.

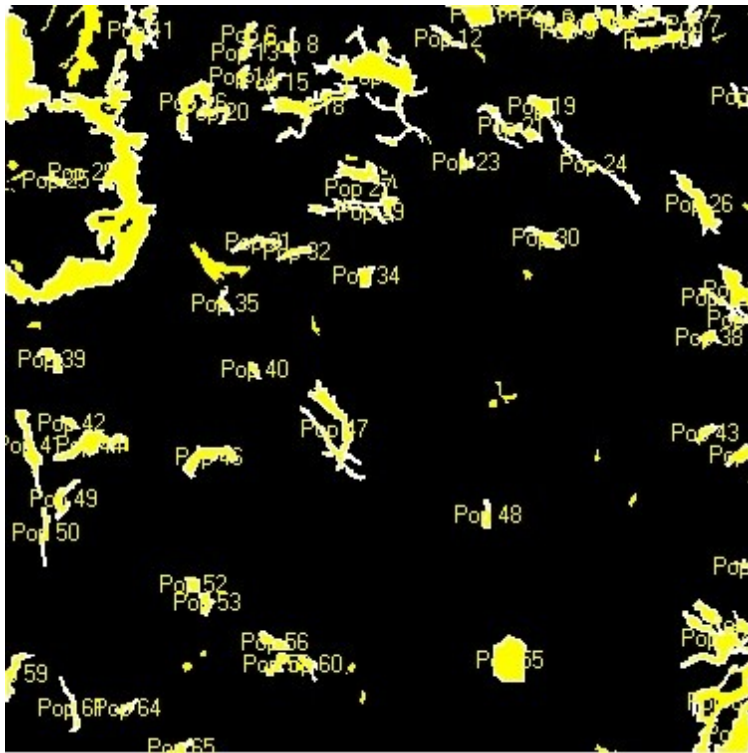


Figure 3.21. Habitat suitability map of *M. avellanarius* for the habitat quality improvement strategy. This landscape scenario assumed that the total amount of fruit-bearing shrub individuals were allocated to the smaller fragments (see text for more details). The yellow polygons represents the woodland fragments. 65 fragments out to the 103 within the squared landscape are occupied by a population.

The 50-year projections of species viability showed that the first, the second and the third landscape scenario returns almost identical predictions on the species persistence, either to the metapopulation abundance at the end of the simulated period (respectively 159, 161 and 160 individuals; Fig. 3.22), and to the probabilities of percentage declines (Fig. 3.23). On the contrary, the fourth landscape scenario, where I allocated the shrub individuals to the smaller fragments, showed a lower terminal metapopulation abundance (148 individuals), and higher probabilities of percentage declines.

Among these set of landscape scenarios, I selected the second one for the following comparison among the three conservation strategies.

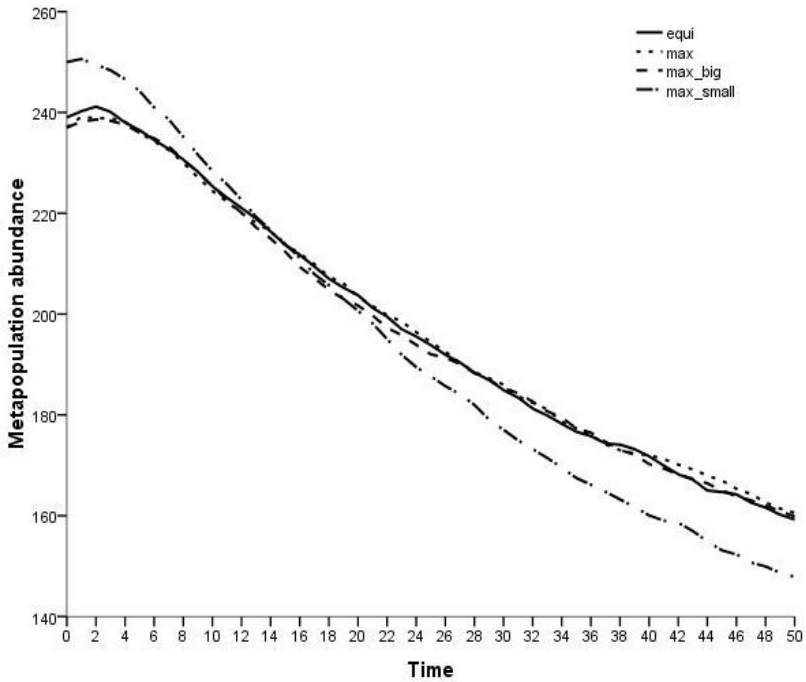


Figure 3.22. Comparison of the results of the metapopulation abundances predicted by the PVAs on the four landscape scenarios for habitat quality improvement. equi = the total amount of fruit-bearing shrub individuals were equally allocated on each 100 m² of habitat; max = the total amount of fruit-bearing shrub individuals were allocated to the fragments with higher nshr values; max_big = the total amount of fruit-bearing shrub individuals were allocated to the greatest fragment; max_small = the total amount of fruit-bearing shrub individuals were allocated to the smaller fragment. See the text for more details on the elaboration of the landscape scenarios.

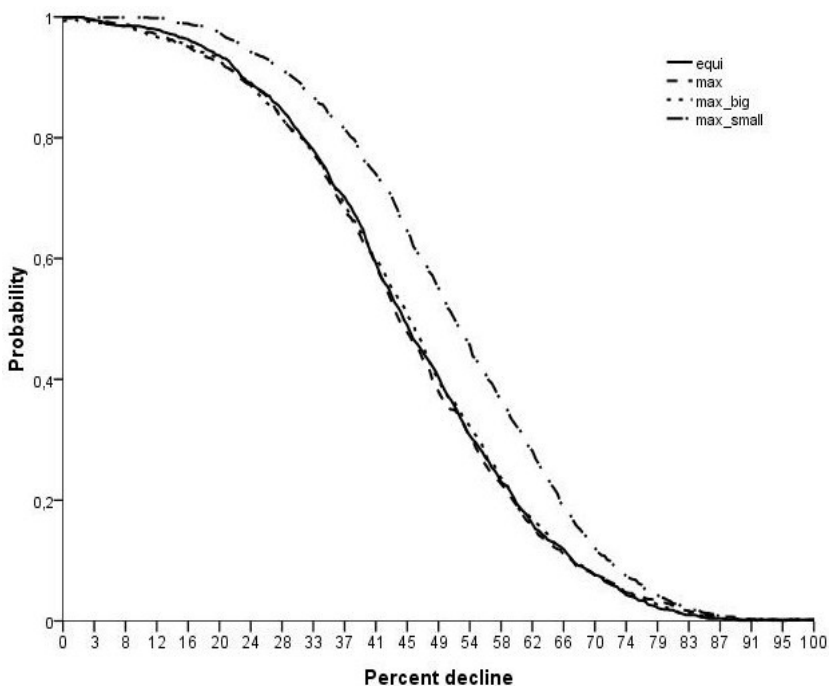


Figure 3.23. Comparison of the results of the probabilities of percentage declines predicted by the PVAs on the four landscape scenarios for habitat quality improvement. equi = the total amount of fruit-bearing shrub individuals were equally allocated on each 100 m² of habitat; max = the total amount of fruit-bearing shrub individuals were allocated to the fragments with higher nshr values; max_big = the total amount of fruit-bearing shrub individuals were allocated to the greatest fragment; max_small = the total amount of fruit-bearing shrub individuals were allocated to the smaller fragment. See the text for more details on the elaboration of the landscape scenarios.

Optimal conservation strategy. The final step of the optimization procedure I elaborated, consist on comparing the first ranked landscape scenarios of each conservation strategy:

- habitat restoration: the afforestation of a single fragment 50 ha sized;
- habitat quality improvement: the plantation of fruit-bearing shrub individuals within the fragments presenting the higher shrub density.

The comparison of the results on the metapopulation abundance showed that the most cost-effective conservation strategy, even though slightly, is to restore 50 hectares of habitat in a single fragment (Fig 3.24).

The comparison of the results on the probabilities of percentage declines showed a similar situation (Fig. 3.25). The two curves proceed with the same trend during the entire simulation period, although the habitat restoration curve showed always slight lower probabilities.

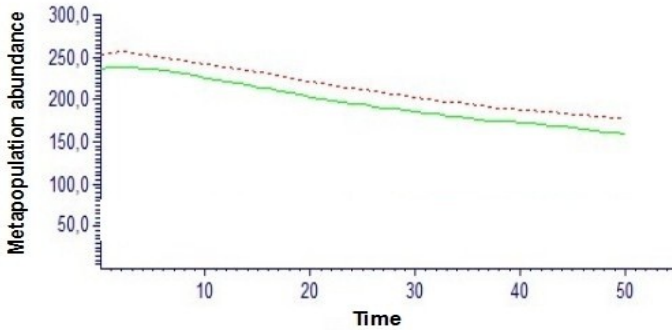


Figure 3.24. Comparison of the results of the metapopulation abundances predicted by the PVAs on the first ranked landscape scenario of each of the three conservation strategies. Green line = habitat quality improvement; red dotted line = habitat restoration.

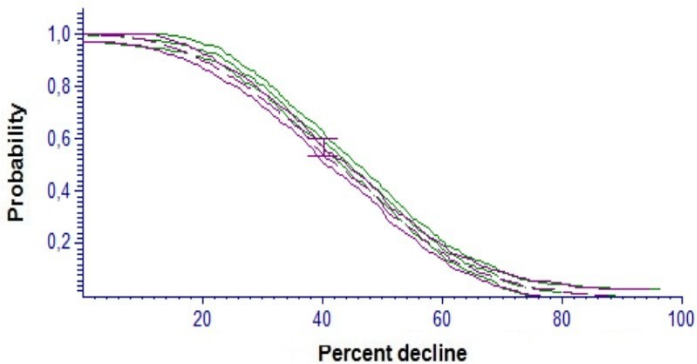


Figure 3.25. Comparison of the results of the probabilities of percentage declines predicted by the PVAs on the first ranked landscape scenario of each of the three conservation strategies. Green line = habitat quality improvement; red dotted line = habitat restoration.

4. DISCUSSION

In the present study emerged that, the two woodland specialist rodent species here investigated, namely the hazel dormouse *M. avellanarius* and the bank vole *M. glareolus*, have different individual and population responses to habitat fragmentation.

In particular, the hazel dormouse vital rates showed a strong relationship with the quality of the fragments (i.e. the complexity of the shrub layer), influencing both the survival rate and the fertility. On the other hand, the bank vole appears to be related to suboptimal quality fragments, with survival rates increasing in smaller fragments and fertility increasing in fragments with lower fruit-bearing shrubs density. Since this species is widely known to be strongly associated to good habitat quality (Geuse et al. 1985), these results may be due to processes not explored in this study, e.g. inter-specific competition.

Likewise, the analysis, which aimed to predict the species persistence in the fragmented landscape, resulted in opposite trends. While the population viability analysis for the hazel dormouse predicted an important decline in metapopulation abundance and occupancy during the 50-year simulated period, the population viability analysis for the bank vole metapopulation showed a marked increase in abundance within the same time interval.

The optimization protocol I elaborated explores which fixed-budget conservation actions would enhance the persistence of the hazel dormouse metapopulation. The protocol allowed to determine that, between the two conservation strategies explored, i.e. habitat restoration and habitat quality improvement, to restore a certain amount of woodlands is the most effective way to increase the metapopulation abundance and to reduce, although slightly, the probability of decline of a given percentage. It is important to note that, however, the optimal conservation strategy would not reverse or prevent the hazel dormouse metapopulation negative trends.

4.1. Reliability of the sampling techniques

The sampling and marking techniques we adopted follow protocols already established both for the bank vole (Gurnell & Flowerdew 1982) and the hazel dormouse (Bright et al. 2006; Juskaitis 2008). In particular, the toe-clipping marking technique used for bank vole is an accepted method frequently applied in field studies, in circumstances where other marking methods are not feasible (e.g. tattoos, leg rings) or not sufficiently permanent (e.g. ear tags). It has been widely documented that this method does not affect the survival of the individual marked (Peacock & Boostra 1985; Fisher & Blomberg 2009; Garner et al. 2011). The multi-year duration of the study, the number of forest fragments sampled and the number of events registered

for the capture or recapture (about 10000) have allowed us to collect a large amount of data, with positive implications to the reliability of the analysis performed.

Regarding the use of the nest-boxes for sampling the hazel dormouse, these are the most effective method for the study of the species (Bright et al. 2006, Juskaitis 2008). The nest-boxes are normally occupied by dormice in all areas across the species distribution, albeit slight seasonal differences might occur. In central and northern Europe dormice occupy the nest-boxes during the whole period of activity (i.e. from spring to autumn, with peaks after awakening and immediately before hibernation), while in the southern Italy the use in the winter months and the partial abandonment in the summer ones has been documented, probably due to changes in hibernation period and the high temperature reached in the nest-boxes in the summer (Sorace et al. 1998, Sarà et al. 2001, Panchetti et al. 2004, Juskaitis 2008). This aspect has implications in the interpretation of the seasonal trends eventually detected in the abundance and density values. Despite this limitation, the species tend to occupy the nest-boxes in a short time (Bright et al. 2006, Juskaitis 2008), to use them as long as weather conditions allow it (i.e. until the outdoor temperature becomes too high or too low), and, above all, to use them for the reproductive activity and for the rearing of offspring, making them a valuable source of information otherwise difficult to obtain.

4.2. The effects of habitat fragmentation on the vital rates of the two species

M. avellanarius

From the capture-mark-recapture data was estimated an extremely low annual survival rate, i.e. 0.001 (s.d. = 0.0006; Tab. 2.5). This means that only the 0.1% of individuals survive from a year to the following, resulting ultimately in a very low figure. Studies conducted on the dormouse in the rest of Europe have found higher annual survival rates (from 0,369 up to 0,655; Juskaitis 2008). Hazel dormouse can live up to 4 years in the wild and up to 6 in captivity (Corbet & Stephen 1991; Bright & Morris 1996).

The annual survival probability and the recapture probability have been modelled as a function of a set of environmental variables. Among the tested models, the one fitted as a function of the number of fruit-bearing shrubs receives a higher support from the data than all other tested models (Tab. 2.4). Previous studies highlighted the great importance of the availability of food resources throughout the year (Juskaitis 2008, Schiavano 2013). I hypothesize that survival rate results for this species may be influenced by this important factor. The abundant fruiting of few shrub species in limited periods of the year which are critical for the biology of the species (e.g. before and after the hibernation), may play a fundamental role in the survival of individuals. The model fitted as a function of the covariates representing the shrub species richness and diversity received very low support (Tab. 2.4),

however, this community indices may not well represent the distribution in time and quantity of shrub fruiting. Unfortunately, both cover indices of selected and not-selected fruit-bearing shrubs species had statistical problems when tested in CMR models (i.e. zero standard errors or unreliable beta estimates). Moreover, since arthropods may be a complementary food resource when other resources are scarce, e.g. late summer and autumn (Juskaitis 2008), the results from the survival analysis may mask the link with the abundance of particular arthropod species related with few shrub species. Future researches on this species should explore these critical topics.

The ranking and selection of the fitted models for inference was performed using the Akaike index (AIC) as a criterion to determine the best model among those examined. This index, however, does not provide an absolute estimate of the accuracy of the model, but only allows establishing a relative rank within a set of candidate models. If a model has statistical support but does not have a recognizable biological sense, this is a sufficient reason to exclude it from the set of models examined (Burnham & Anderson 2002). In the present study, within the set of models examined for each species, all models having a ΔAIC_c less than 1 were considered plausible.

In this research the mean litter size for dormice was 3.3 (s.d. = 1.64). In comparison with other rodents, the reproductive output of this species is rather limited (Juskaitis 2008). The results showed that, in the investigated area, the mean litter size is the lowest ever recorded across the entire distribution area of the species. In fact, the average size of the

litter for the species is approximately 4 juveniles (Juskaitis 2008). The largest mean litter size the dormouse has been recorded in England, with more than 5 juveniles (Eden & Eden 2001). In Lithuania, the average litter size was found to be 4.07 (Juskaitis 2008), while in Western Russia is 4.5 (Likhachev 1966), in line with the results from this research. The maximum litter size ever recorded is 9 juveniles (Lozan 1970).

The influence of food availability on female reproductive effort is considerable (Matter et al. 2009), so that the abundance of food resources has been regarded as a possible limiting factor for the persistence of species in fragmented landscapes (Zanette 2000, Zanette et al. 2000). In particular, there may be a minimum threshold of trophic availability below which the food resources would become insufficient to allow survival and reproduction of individuals. In this case, the populations may settle in suboptimal habitat fragments and may suffer a decline in abundance until reaching local extinctions (Lynch & Whigham 1984; Burke & Nol 1998).

Consistently with my predictions, in the first two ranked regression models, fertility was modelled as a function of the number and cover of fruit-bearing shrub species (Tab. 2.6). It is important to note that the food abundance index, which represents the grouped cover of selected fruit-bearing shrub species (*abshr_sel*), is poorly supported by the data, although these shrub species are known to constitute a great part of the hazel dormouse diet (Amori et al. 1993; Bright et al. 2006; Juskaitis 2008). This counter-intuitive results might be explained by the greater importance of a more diversified availability of food resources

during the year respect to a greater abundance of less shrub species fruiting in a narrow temporal interval.

M. glareolus

The annual survival probability of bank vole was extremely low, i.e. 0.012 (s.d. = 0.004; Tab. 2.8), consistently with the rapid replacement rate of this species and its short-lived life trait (generally less than one year under natural conditions, with a minimum of 2-3 months in conditions of high densities; Corbet & Stephen 1991).

The CMR analysis I performed highlighted a negative relationship between the survival rate of the bank vole and the fragment size (Tab. 2.7). Despite the strong specialist habits of the species (Geuse et al. 1985), and the presumed limited dispersal ability (Kozakiewicz et al. 1999), Mortelliti et al. (2009b) found bank vole inhabiting small woodland fragments in highly modified landscapes. In the present research the species was found in all fragments of small size. The only two fragments where bank vole was not found at all were those of relatively big size (between 10 and 15 hectares). In the second ranked model, although with a ΔAIC beyond the assumed threshold for inference, the survival probability was negatively correlated with the abundance of acorns, the main food resource of the species (Hansson 1998). In synthesis, in greater fragments with higher habitat quality the bank vole has a lower probability to survive from one year to the following then in smaller fragments with worse habitat quality. In order to explain these unexpected results, I hypothesize a “masked” effect. I

suggest that the “negative effect” of an increase in fragment size and quality is an indirect correlation due to the effects of the interspecific competition with the yellow-naked woodmouse *Apodemus flavicollis*. In fact, the yellow-naked woodmouse is a woodland specialist with habitat requirements very similar of those of the bank vole, i.e. complex shrub layer in the understorey and availability of seeds (Stenseth 1985, Pucek et al. 1993, Jędrzejewski & Jędrzejewska 1996, Stenseth et al. 2002). The direct and indirect competition for nesting and food resources between the two rodent species is widely documented (Ylönen et al. 1991, Ebensperger 2001, Wolff & Sherman 2007), and it seems that bank vole tends to colonize empty fragments where the yellow-naked woodmouse had been removed (Ylönen et al. 1991). Therefore, I suggest that, in the fragmented area where I carried out the present study, the interspecific competition penalizes bank voles in better quality woodland fragments (i.e. lower edge effect and higher abundance of acorns). During the sampling session of this study we performed further trapping of yellow-naked woodmice, and future analysis may investigate my hypotheses.

Previous researches highlighted how the reproductive success of *M. glareolus* may be influenced by the availability of food resources (Oskanen et al. 2001, Koivula et al. 2003, Mappes & Koskela 2004; see also Haapakoski & Ylönen 2010 for a conflicting result). Also the presence and distance of proximate populations showed to influence the species breeding dynamics (Kozakiewicz et al. 2007, Trebatická et al. 2008, Haapakoski & Ylönen 2010).

In the present study I found that the fertility was negatively correlated with the density of shrub plants (Tab. 2.9). One possible explanation for these conflicting results follows the consideration reported above for the survival analysis. In spite of the widely documented importance of the habitat quality for the breeding success of this species, the fertility rate of *M. glareolus* may be lower in higher quality fragments because in these the species may not fully exploit the available resources due to the competition with *A. flavicollis*.

Another explanation for such results is that there is an influence of environmental factors, but it has not been detected due to the limited sample size available for the estimate of this parameter (data coming from only nine fragments; Appendix III, Tab. 2). The low goodness-of-fit of the tested models (Tab. 2.9) seems to confirm the inadequacy of the available data for this analysis. It should be emphasized that, in a study on small mammals using trapping *in vivo*, fertility is a parameter whose data collection is considerably complex. In particular, in the present research the fertility data was collected opportunistically from females died accidentally during the trapping sessions. Moreover, it is important to highlight that the reproductive effort and breeding success of the bank vole showed to be affected also by unbalanced sex ratios towards males (Mappes et al. 2008), and by social constrains (Prevot-Julliard et al. 1999).

Further analysis will be needed to explore those topics.

4.3. Reliability of the SEPMS parameterization

The spatially explicit population viability analysis carried out with RAMAS GIS software combines spatial data on the landscape with habitat requirements of the species and demographic data into a metapopulation model. The reliability of the long-term measures of threat and viability predicted by the metapopulation models strongly depends on the quality of the short-term data (Jäkäläniemi et al. 2013). In the present section, I discuss the strengths and weaknesses of the procedure I used to parameterize the SEPMS of hazel dormouse and bank vole metapopulations.

The Habitat Suitability (HS) function is defined in RAMAS GIS as any quantitative relationship between physical and biological factors in the environment and the suitability of the environment for a given species (Akçakaya 2005). The definition is not limited to any specific functional form or to any specific statistical procedure used to obtain the relationship (Akçakaya 2005). Some authors built the habitat suitability maps by interpolating presence data of the species with GIS-generated maps of habitat characteristics or land uses (Root 2004, Yamada et al. 2004); other authors applied occupancy models on presence-absence data (MacKenzie et al. 2006) in order to obtain a logistic regression function to use as HS function (Sachot & Perrin 2004, Fipaldini 2012, Roviani 2013). Similarly to Breininger et al. (2004), in the present research I defined the HS functions as a different map layer for each species, representing the two habitat characteristics which resulted to influence the survival rate of the species. My purpose was to obtain a

metapopulation map for each species which would represent a plausible starting point, in terms of the number of populations detected in the landscape, for the following simulations. Therefore, for the hazel dormouse each fragment suitability is defined by the respective value of the covariate *nshr*, while for the bank vole each fragment suitability is defined by the respective value of the covariate *logha* (Tab. 3.1). By definition, I set the HS thresholds as the minimum value of the covariates in fragments where reproductive events were recorded (Tab. 3.1). The comparison between the proportion of fragments where reproductive events were recorded (0.55 for the hazel dormouse and 0.97 for the bank vole) and the proportion of detected populations with respect to the total number of fragments in the landscape sampled in the first session (0.52 for the hazel dormouse and 0.9 for the bank vole), confirms the reliability of this approach.

As regard to the vital rates, i.e. the survival rate and the fertility, the majority of authors tends to parameterize them in RAMAS GIS with the estimates obtained from the analysis of capture-mark-recapture data, in the case of the survival parameterization, and with mean litter size calculated on field of bibliographic data, in the case of the fertility parameterization (e.g. see the several works in Akçakaya et al. 2004). Some of the abovementioned studies were carried out in continuous habitat (Brook & Griffiths 2004, Hatfield et al. 2004) and this could justify the use of a single estimate to parameterize more than one population. However, in fragmented habitat where the habitat relationships with the vital rates are known, as in the case of the present

research, I argued that setting the survival and fertility rates (and, perhaps, as many parameters as possible) with the regression or logistic models is the most effective way to incorporate the demographic stochasticity and the spatial variation of these parameters. The reliability of the tested models and of the estimated parameters was discussed in the previous paragraph.

The maximum growth rate of the population of the two species was set with a value greater than 1 (Tab. 3.1). This would suggest that the metapopulations of hazel dormouse and bank vole are actually in an increasing phase. However, when the growth rate of a population is calculated with data gathered in a short period (e.g. two years), it may describe only the current status of the population and not a reliable future trend. Moreover, when the growth rate observed is more than 1, this may indicate that: 1) the population may be under the influence of stochastic fluctuations caused by environmental factors; 2) the population may have temporarily exceeded the carrying capacity of its habitat and may have declined due to density-dependence mechanisms (Akçakaya 2005). These are the main reason why I omitted negative values when calculating this parameter. It is important to emphasize that the average growth rate of the population is a mean. In some areas the rate was found to be positive, while in others negative, suggesting a source-sink dynamics in populations under investigation. In the calculation of the present research, by omitting negative growth rates, sink dynamics were probably underestimated. However, since I aimed to compare not the absolute but the relative performance of different

landscape scenarios, I feel confident that such bias would not negatively affect the results and implications of my comparisons.

The estimates of the carrying capacity and of the initial abundance in this research was based on the fragment size (Shriver & Gibbs 2004), and the density values observed in the populations investigated, an approach commonly adopted by several authors (Griffin & Mills 2004, Lopez 2004; Gerber 2004). This methodology is based on the assumption that the spatial variability of the abundances of current populations reflects the temporal variability of the abundances of populations. In fact, getting a time series of the population densities, is possible to estimate quite precisely its carrying capacity (Sezen et al. 2004).

Another type of approach to implement the carrying capacity in the SEPMS involves the use of the home range. In this case, the carrying capacity is calculated by the ratio between the size of the fragment and the average size of the species home range (Root 2004). In fact many species in nature, as the bank vole and the hazel dormouse, have home ranges partially overlapped. Therefore, to be realistic, this approach should consider also the degree of overlap between home ranges (Akçakaya & Raphael 1998). In this research, since I had not data on the overlapping for the home ranges of the two species, I used the first described approach.

The dispersal dynamics plays an important role in the persistence and vitality of spatially structured populations (Akçakaya et al. 1995; Lopez 2004; Wintle et al. 2005, Fowler 2009, Harrison et al. 2013). In

agreement with the dispersal-distance function, the approach followed in this research involves estimating the rate of dispersion among populations as a function of the distance that separates the two populations (Akçakaya 2005). The distance between two populations was calculated as the closest distance between the edges of the concerned fragments. This approach is based on the assumption that the probability that an individual in dispersion reaches another patch is a function of the distance it has to travel (Possingham & Davies 1995; Lindenmayer et al. 2001; Root 2004; Sezen et al. 2004; Wintle et al. 2005).

The distances of dispersion of a species are usually estimated through the use of radio-tracking data (Akçakaya & Raphael 1998; Lindenmayer et al. 2001; Griffin & Mills 2004; Root 2004). However, the gathering of this kind of data requires a great field effort, since it is necessary to have a very large sample of individuals to obtain accurate and realistic distance estimates. Another method to estimate this parameter is the use of capture-mark-recapture data (Bright 1998, Buchner 2008). In this research I adopted a distinct approach for each species in order to parameterize the maximum dispersal distance of the dispersal-distance function.

In the approach adopted for the hazel dormouse, I measured the longest distance that separate an isolated fragment (i.e. in absence of any hedgerow or linear structure connecting or not the focal fragment to another) where we recorded a colonization event, to the nearest fragment assumed to be occupied. Since the exact identification of the

source fragment was not possible, the colonizer could have covered a longer distance. Therefore, that is a conservative measure.

As regards the bank vole, I was able to estimate a mean dispersal distance from a set of recorded migration events of marked individuals. As in the previous case, I preferred to use the mean value rather than the maximum value in order to be conservative.

Another parameter of the dispersal-distance function is the proportion of individuals that migrate from one population to another. The majority of the researches that investigate the dispersal dynamics of the species, were carried out within a continuous habitat (i.e. not among fragments; Szacki & Liro 1991, Bright et al. 1994, Bright & Morris 1996; Kozakiewicz et al. 2007, Buchner 2008; Juskaitis 2008; Wolton 2009). Therefore, the mechanisms of movement and dispersion of the two species in the matrix are practically unknown. The only works to this respect are those of Bright (1998) and Buchner (2008) on hazel dormouse dispersion. However, their results are not appropriate for a correct parameterization of the parameter in question, as they not provide the number of individuals moving from a population to another. In this research, facing the inability to obtain an estimate of this parameter, an expert opinion (Mortelliti pers. comm.) was used for both species: that is a realistic and conservative value, for which a very low proportion of individuals leave the patch ($a = 0.01$; Par. 3.1.1). The approach of using an expert guess is widely applied in literature (see Root 1998, Yamada et al. 2004, Wintle et al. 2005), and few studies used, at today, radio-tracking data for the estimation of this parameter

(Haines et al. 2006; Lopez 2004).

For a correct parameterization of the SEPMS, it is a priority to get empirical evidence on how individuals move from one population to another. Radio-tracking techniques are unlikely to record the movement of a small mammal from a fragment to another, due to the limited duration of the radio collars. Therefore, the best way to get an accurate estimate of the proportions of individuals that goes in dispersion from one population to another, is to use the results of genetic tests on microsatellite loci (Lethbridge et al. 2001).

4.4. Optimization framework for the selection of conservation strategies: values, limits and future perspectives

In a socio-economic context of limited financial funds, as that experienced by conservation biology, it is essential that, following the setting of conservation objectives (Nicholson & Possingham 2006, Sanderson 2006), the capital available for management actions be used to maximize the ecological returns (Joseph et al. 2009, Moilanen & Wilson 2009).

In the present research, I elaborated an optimization framework in order to explore the performance, in terms of the two target rodents metapopulations persistence, of two conservation strategies (namely, habitat restoration and habitat quality improvement), accounting for the management costs of each strategy, with a fixed available budget of 1 million of euros. By combining i) a metapopulation persistence analysis through the use of SEPMS based on spatially explicit PVAs, and ii) a

decision-making protocol based on management scenarios simulations (Dreschler et al. 2003, Dreschler & Burgman 2004, Schumaker et al. 2004, Baxter et al. 2006, Drielsma & Ferrier 2006), I was able to compare and rank the relative efficiency of the three abovementioned conservation strategies.

The framework has three main simplifications. First, I started the framework building by assuming a fixed available financial budget, and then elaborated the simulation protocols in order to answer to the question: how can I spend this money achieving the maximum biological return? In more complex scenarios, the decision-making procedure may be integrated in a dynamic resource allocation framework (Haight & Travis 1997, Wilson et al. 2006, McCarthy et al. 2008). Within this context, a widely used approach is the maximization of the return of investment (Possingham et al. 2000; Murdoch et al. 2007, 2010; Underwood et al. 2008), particularly in the detection of priority areas where to focus the allocation of conservation resources (Wilson et al. 2007, Bode et al. 2008), and in the identification of the more cost-effective invasion control strategy (Baxter et al. 2008, Capizzi et al. 2010, McDermott et al. 2013). Return of investment protocols measure the conservation gain by selecting the options that maximize the conservation return per unit of investment. A similar procedure would allow the detection of the optimal set of strategies which, at the same time, minimize the costs.

Second, the cost-effectiveness of the two conservation strategies here considered was explored once at a time. Moreover, I applied the

optimization framework to the target species separately. In future investigations, should be analysed the consequences in the metapopulations responses of the implementation of more than one strategy (i.e. restoring a certain amount of forests while improving the quality of those existing; Tambosi et al. 2013), adopting a multicriteria approach (e.g. maximize together the persistence of both species; Akçakaya 2000b, Estevez et al. 2013).

Third, for simplicity I assumed static habitat scenarios in the simulation protocols. In the habitat restoration and quality improvement scenarios, the effects of these strategies arose immediately, without taking into account the time lags needed for vegetation maturation. The habitat dynamics and the time lag in vegetation maturation are critical knowledge gaps in optimal planning of vegetation restoration in future landscapes (Vesk & MacNally 2006, Possingham et al. 2009). The restoration and improvement scenarios do not take into account the temporal dynamics and the time lags in vegetation maturation, probably leading to the overestimate of species persistence results within a specified time frame. RAMAS GIS allows the modelling of temporal dynamics in habitat amount and characteristics through the implementation of the Habitat Dynamics subprogram in the simulation procedure (Akçakaya et al. 2004, Larson et al. 2004, Schtickzelle & Baguette 2004, Keith et al. 2008). Therefore, as a future perspective, the ultimate goal is to integrate both spatial and temporal dynamics into the frameworks for making optimal decisions for replanting natural vegetation that takes into account time-lags in vegetation development

and the time course of providing ecological resources.

Moreover, the conservation resource allocation framework is underpinned by region-specific characteristics, such as the cost of conservation actions (e.g. the land values) and the local biology of the target species (e.g. the longer activity season of hazel dormouse respect to northern populations; Panchetti & Carpaneto 2005, Juskaitis 2008).

In this study, I explored the cost-effectiveness of two management strategies: the forest restoration (Munro et al. 2007, Aronson & Alexander 2013) and the forest quality improvement (Gómez-Aparicio et al. 2004, Padilla & Pugnaire 2006, Smit et al. 2008). However, the optimization framework I presented here may be applied in different management situations, and should help to address important ecological, conservation, and management problems that deal with species persistence, not only in fragmented landscapes. In extended and continuous forest landscapes, sustainable forest management strategies should be considered (Wintle et al. 2005). As an example, the improvement of the forest quality, in terms of the shrub layer enrichment, may be achieved by clearings creation through selective logging (McCarthy & Lindenmayer 1998, Nalle et al. 2004, Semlitsch et al. 2009). In this context, the optimization framework should incorporate not only the logging costs, but also the timber harvest incomes (Calkin et al. 2002).

In fragmented landscapes, the present framework may be applied to deal with the “matrix matter” (Ricketts 2001). Due to the great influence of the matrix permeability on dispersal success of spatially

structured populations (Ray et al. 2002, Schooley & Wiens 2004, Castellòn & Sieving 2006, and the review of Prevedello & Vieira 2010), and the high dynamism of agricultural landscape (Keimer et al. 2000), the ability to predict population responses to land uses changes is an important issue. The application of the framework, through the simulation of future landscape scenarios where different land use changes are predicted (Montgomery et al. 1999, Schumaker et al. 2004, Polasky et al. 2005, 2008), should allow to determine the optimal combination of land uses in the matrix which would increase its permeability, thus facilitating the inter-patch movements of individuals and the metapopulation persistence (Johst et al. 2002).

A further important value of the present framework lies on the possibility to detect those demographic parameters which play a fundamental role in determining the SEPMs results. Performing sensitivity analysis (Wintle et al. 2005, Haines et al. 2006, Naujokaitis-Lewis et al. 2009), incorporated in RAMAS GIS in a specific subprogram, make possible the detection of those critical parameters. As an example, I performed sensitivity analysis on three important parameters of the hazel dormouse SEPM: the maximum growth rate, the carrying capacity and the dispersal rates. In order to explore the sensitivity to relatively small changes, I simulated the metapopulation response of this species to changes of these parameters of +10%, +30% and +50% (Fig. 4.1). The sensitivity analysis on dispersal rates showed, both for the metapopulation abundance trend and the probability of a percentage decline, that the simulation results are relatively insensitive

to the uncertainty of this parameter. On the opposite, even a small bias in the estimates of the maximum growth rate and in the carrying capacity would determine a great change in the SEPMS predictions, especially in the predicted probabilities of percentage decline. The results of these sensitivity analysis suggest that, in order to achieve an higher accuracy and reliability of the SEPMS predictions, a particular attention should be payed in the data gathering and the following estimation of these two critical parameters. Since in the present research data were gathered in a 2-3 years period, the estimates of these parameters may be biased due to demographic stochasticity here not considered. As a consequence, a longer field effort may guarantee an higher precision and reliability of the paramter estimation.

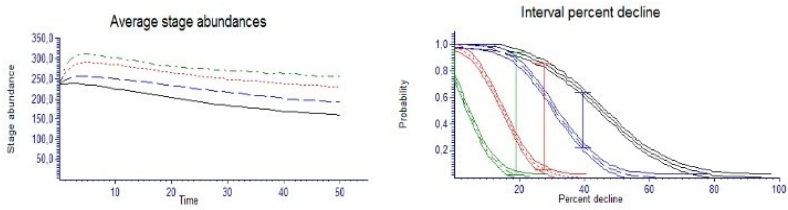
Ultimately, this uncertainty analysis may supply important guidelines for further deeper investigations, inserting this optimization framework in a more general framework of adaptive management (Schreiber et al. 2004, McDonald-Madden et al. 2010).

Finally, this framework, due to the combination of demographic data gathered on the field with a sophisticated modelling approach, make it a reliable instrument in supplying clear insights and information to help in addressing optimal investments, thus representing a useful and practical evidence-based criterion to support the decision-making processes (Pullin et al. 2004, Sutherland et al. 2004, Pullin & Knight 2009).

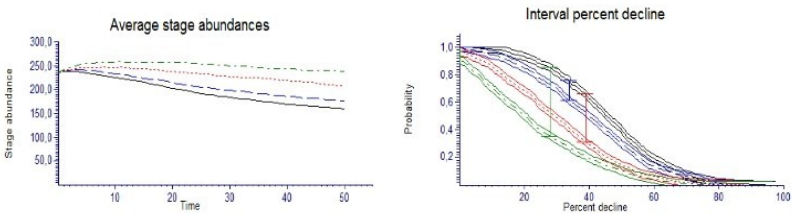
The identification of the optimal conservation strategies using both biological and non biological factors is currently in its infancy

(McBride et al. 2007). Researches on how the combination of biological, economic, social, and political factors would influence the choice of investment, and the realized returns remains a priority in conservation biology (Naidoo et al. 2006, Cook et al. 2013).

Sensitivity analysis on maximum growth rate (Rmax)



Sensitivity analysis on carrying capacity



Sensitivity analysis on dispersal rates

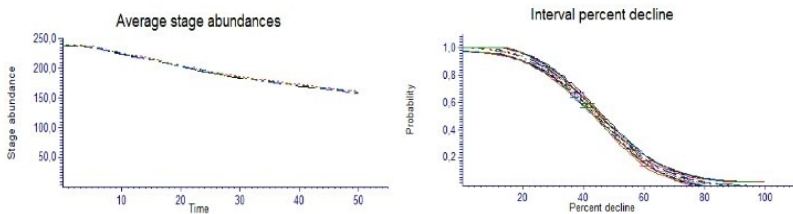


Figure 4.1. Results of sensitivity analysis on maximum growth rate (Rmax), carrying capacity (K) and dispersal rates of hazel dormouse. Black line = standard parameters; blue dashed line = +10% change; red dotted line = +30% change; green dashed-dotted line = +50% change.

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APPENDIX I

Table 1. Values of fragment and neighborhood covariates. *M.ave.* = *Muscardinus avellanarius*; *M. gla.* = *Myodes glareolus*. See Par. 2.1.3 for covariates description.

Fragment and neighborhood covariates								
<i>M.ave.</i>	<i>M.gla.</i>	ha	logha	par	neardist	hdgxpch	hdg_con	pch_con
-	MG1	0,56	0,19	0,0516	172,9	5	0	0
-	MG2	0,75	0,24	0,0634	639,47	1	1	2
-	MG3	0,83	0,26	0,0614	6,39	3	2	2
-	MG4	1,01	0,3	0,0479	271,36	2	0	0
-	MG5	1,05	0,31	0,0479	271,36	2	0	0
-	MG6	1,2	0,34	0,0413	639,47	1	0	0
MA1	MG7	1,2	0,34	0,0420	393,46	3	1	1
-	MG8	1,46	0,39	0,0370	237,36	5	0	0
MA2	MG9	1,74	0,44	0,0372	882,52	5	0	0
-	MG10	2,26	0,51	0,0419	435,38	5	0	0
MA3	MG11	2,55	0,55	0,0355	1217,83	2	0	0
-	MG12	2,74	0,57	0,0242	38,94	7	1	1
-	MG13	2,85	0,59	0,0317	1034,85	2	3	3
MA4	MG14	2,87	0,59	0,0388	117,07	8	4	2
-	MG15	3,54	0,66	0,0307	50,25	5	0	0
MA5	-	3,8	0,58	0,0248	590,21	6	3	7
-	MG16	4,38	0,73	0,0411	117,07	8	2	1
-	MG17	4,72	0,76	0,0258	50,25	7	0	0
-	MG18	5,07	0,78	0,0330	65,17	8	3	3
MA6	MG19	5,72	0,83	0,0252	393,46	3	3	2
-	MG20	5,73	0,83	0,0197	181,06	6	4	3
-	MG21	9,66	1,03	0,0421	181,06	7	1	2
-	MG22	10,64	1,07	0,0209	763,5	5	1	1
-	MG23	11,71	1,1	0,0239	433,94	9	3	3
-	MG24	12,81	1,14	0,0221	79,31	9	1	1
-	MG25	13,65	1,17	0,0211	724,03	5	3	5
-	MG26	14,08	1,18	0,0206	64	11	7	5
-	MG27	17,21	1,26	0,0379	90,29	10	10	4
MA7	-	21,5	1,33	0,0083	1269,19	5	3	7
MA8	MG28	22,09	1,36	0,0300	584,32	4	0	0
MA9	MG29	233,91	2,37	0,0093	12,91	18	6	4

Fragment and neighborhood covariates							
<i>M.ave.</i>	<i>M.gla.</i>	ha_pch_con	pch_buff721	ha_buff721	ha_buff497	pch_buff497	log_sem
-	MG1	-	5	6,53	-	-	2,441
-	MG2	-	1	1,2	-	-	2,518
-	MG3	-	2	2,55	-	-	2,534
-	MG4	-	2	2,97	-	-	2,485
-	MG5	-	3	4	-	-	2,565
-	MG6	-	1	0,75	-	-	2,510
MA1	MG7	5,724	1	5,72	100,079	1	2,498
-	MG8	-	3	41,34	-	-	2,254
MA2	MG9	22,025	2	4,05	108,911	0	2,283
-	MG10	-	2	10,4	-	-	2,505
MA3	MG11	62,009	0	0	123,506	0	2,592
-	MG12	-	2	3,36	-	-	2,467
-	MG13	-	1	13,76	-	-	2,485
MA4	MG14	8,171	6	17,1	131,442	3	2,446
-	MG15	-	4	8,02	-	-	2,496
MA5	-	62,94	-	-	0	0	-
-	MG16	-	4	20,17	-	-	2,371
-	MG17	-	5	8,87	-	-	2,514
-	MG18	-	5	28,38	-	-	2,396
MA6	MG19	22,794	1	1,2	146,719	1	2,567
-	MG20	-	4	13,9	-	-	2,533
-	MG21	-	6	15,04	-	-	2,631
-	MG22	-	1	0,83	-	-	2,466
-	MG23	-	8	30,19	-	-	2,540
-	MG24	-	4	22,15	-	-	2,196
-	MG25	-	3	8,33	-	-	2,345
-	MG26	-	5	18,97	-	-	2,578
-	MG27	-	9	24,71	-	-	2,679
MA7	-	98,844	-	-	0	0	-
MA8	MG28	44,270	2	2,64	291,015	0	2,642
MA9	MG29	339,097	14	127,52	928,518	8	3,032

Table 2. Values of fragment vegetation structure covariates. *M.ave.* = *Muscardinus avellanarius*; *M. gla.* = *Myodes glareolus*. See Par. 2.1.3 for covariates description.

Vegetation structure covariates									
<i>M.ave.</i>	<i>M.gla.</i>	nalb	mbbh	canopy	erb	lett	rich	shan	volarb
-	MG1	1,88	29,53	4,38	2,75	3,75	12	0,922	11,63
-	MG2	7,25	14,57	5,88	0,75	3,63	13	1,009	11,5
-	MG3	6,75	16,56	5,25	1,88	3,63	10	0,808	8,25
-	MG4	12,63	13,25	7,88	3,75	3,13	13	0,985	8,88
-	MG5	7	17,13	3,5	3,25	3,25	16	1,100	9,63
-	MG6	12,86	12,24	7,43	1,29	4	13	0,988	8,86
MA1	MG7	14,31	14,93	5,91	2,43	3,8	13,5	1,048	13,2
-	MG8	13,29	12,64	4,86	3,14	3,86	14	1,039	4,43
MA2	MG9	21,06	10,62	6,87	2,16	3,68	15,5	1,116	9,79
-	MG10	17,25	13,22	7,75	1,5	4	10	0,935	3,25
MA3	MG11	18,19	9,39	6,19	1,47	3,83	13	1,028	10,22
-	MG12	8,88	12,07	1,88	1,67	3,17	14	1,052	13,5
-	MG13	7,88	20,17	6,13	3	3,13	14	1,002	9,63
MA4	MG14	11,9	10,51	6,01	2,92	3,45	15,5	1,104	8,15
-	MG15	9,88	14,28	6	3	3,63	12	0,968	7,38
MA5	-	18,31	11,68	6,13	1,75	3,81	13	0,98	9,75
-	MG16	19,63	13,74	8	2,25	3,13	15	1,089	6,63
-	MG17	3,5	25,42	6,25	3,75	3,38	16	1,076	6,13
-	MG18	5,63	14,38	1,88	1,25	3,63	12	0,977	12,75
MA6	MG19	13,55	13,77	4,8	2,72	2,61	15,5	1,117	6,72
-	MG20	9,78	14,57	4,44	2,5	3,88	12	0,926	12,89
-	MG21	10	14,41	3,71	2,14	4	14	1,037	12,43
-	MG22	10,88	11,09	4,63	1,88	3,13	15	1,106	8,88
-	MG23	14,13	9,1	7,25	2,5	3,33	15	1,041	13,25
-	MG24	13,13	11,59	6,25	3,5	3,83	9	0,858	2,88
-	MG25	18,5	11,35	6,38	1	3,75	13	1,05	7,63
-	MG26	26,38	9,84	7,63	1,4	3,4	12	1,01	7,63
-	MG27	10,13	10,24	6,13	2,86	3,71	11	0,915	12,5
MA7	-	14,46	8,01	3,19	1,04	3,88	13	1,03	12,04
MA8	MG28	19,9	11,83	6,39	2,74	3	18,5	1,179	7,28
MA9	MG29	14,04	8,53	5,21	1,67	3,64	15,5	1,084	12,09

Table 3. Values of fragment food resource covariates. *M.ave.* = *Muscardinus avellanarius*; *M. gla.* = *Myodes glareolus*. See Par. 2.1.3 for covariates description.

Food resource covariates							
<i>M.ave.</i>	<i>M.gla.</i>	nshr	abshr	abshr_sel	gh_cer	gh_rov	gh_tot
-	MG1	4,88	7,88	4,38	25,66	7103,69	7129,35
-	MG2	8,13	11,38	8,13	0	1057,54	1057,54
-	MG3	5,25	8,63	5,25	0	379,12	379,12
-	MG4	7,63	10,5	7,13	0	289,45	289,45
-	MG5	7,88	11,75	7,75	0	0	0
-	MG6	7,71	11,21	7,71	131,92	254,65	386,57
MA1	MG7	7,44	11,19	8,07	8,41	4,8	13,22
-	MG8	5,43	6,57	3,86	200,96	517,46	718,42
MA2	MG9	7,89	10,82	7,35	493,77	18,08	511,85
-	MG10	5,38	5,25	4	414,87	407,58	822,45
MA3	MG11	7,06	9,86	7,28	291,06	0	291,06
-	MG12	11	19,5	13,13	183,71	0	183,71
-	MG13	8	11,5	6,88	689,19	1207,89	1897,09
MA4	MG14	5,89	8,3	4,97	86,26	0	86,26
-	MG15	7,13	9,5	4,75	646,77	258,39	905,16
MA5	-	6,69	9,13	6,38	-	-	-
-	MG16	7,13	8,63	5,75	150,52	5,78	156,3
-	MG17	9,13	12,75	7,25	0	2158,57	2158,57
-	MG18	7,13	11,38	7,38	368,84	0	368,84
MA6	MG19	6,53	7,73	5,89	54,89	65,79	120,68
-	MG20	7	11,56	7,33	946,04	151,49	1097,53
-	MG21	8,43	12,14	8	377,59	873,74	1251,34
-	MG22	7	10	5,13	149,73	83,84	233,57
-	MG23	7,63	9,63	6,25	1082,27	7,82	1090,08
-	MG24	4,38	5	2,5	0	480,56	480,56
-	MG25	8	10	7,00	536,71	522,88	1059,59
-	MG26	7,63	10,13	7,00	902,23	42,2	944,43
-	MG27	6,63	10	8,75	72,07	453,54	525,61
MA7	-	6,81	8,54	7,08	-	-	-
MA8	MG28	8,93	11,2	6,86	378,66	0	378,66
MA9	MG29	8,15	10,19	7,8	859,65	0	859,65

Food resource covariates

<i>M.ave.</i>	<i>M.gl.a.</i>	ruscus	crataegus	cornus	rosa	rubus	prunus	ligustrum
-	MG1	0,38	0	0,63	0,25	2,5	0	0,13
-	MG2	0	1	1,13	0,5	2,63	0,88	1,25
-	MG3	0,13	0,13	0	0,63	2,5	1,38	0,13
-	MG4	0	1	0,25	1	1,5	2,5	0,63
-	MG5	0,13	0,38	1	1	1,38	1,75	0,5
-	MG6	0	1,14	0,71	0,43	1,71	2,43	0,71
MA1	MG7	0	0,85	1,09	0,86	1,55	2,37	0,99
-	MG8	0	0,14	0,29	0,29	1,29	0,57	0,57
MA2	MG9	0,59	0,59	1,35	0,48	1,89	0,48	1,59
-	MG10	0,13	0,5	0,63	0,88	0,75	0,25	0
MA3	MG11	0,49	0,99	0,42	0,63	0,69	0,79	2,46
-	MG12	0,88	1,38	1,63	1,88	2,38	1,13	3,13
-	MG13	0,25	1	0,88	0,38	1	0,25	2,63
MA4	MG14	0,05	0,23	0,77	0,57	0,7	1,38	0,85
-	MG15	0,38	0,13	0,63	0,75	1,38	0	0,88
MA5	-	0,13	0,63	1	0,31	1,44	0,56	1,94
-	MG16	0,25	0,63	0,88	0,75	0,5	1,5	1
-	MG17	0,38	0,38	2,13	0,88	1	0,38	1,75
-	MG18	0,63	0	1,25	0,75	2,63	0,13	1,5
MA6	MG19	0,79	0,83	0,75	0,74	0,86	0,73	0,85
-	MG20	0,11	1,89	0	0,33	0,67	0,33	3,22
-	MG21	0,86	1,14	0	0,43	2,29	0,57	1,86
-	MG22	0,5	0,38	0,75	0,88	1	1	0,13
-	MG23	1	0,5	1,88	0,38	1,5	0,25	0,63
-	MG24	0	0	0,13	0,38	0,5	0	0,5
-	MG25	0,63	0,88	0,25	1,13	1,13	1,38	1,13
-	MG26	1,13	0,25	0,5	1	1	1,75	0,13
-	MG27	0	2,13	1,75	0,38	0,63	1,63	1,38
MA7	-	0,15	1,23	0,69	0,5	1,04	1,81	1,12
MA8	MG28	1,02	0,85	1,04	0,66	0,87	0,55	1,33
MA9	MG29	0,59	1,11	1,82	0,6	1,18	0,94	1,03

APPENDIX II

Table 1. Correlations among all covariates used in survival and fertility analysis on both *M. avellanarius* and *M. glareolus* analysis.

Covariates correlations										
	nalb	can	lett	narb	shan	gh_rov	volarb	par	pch_buff7:	
	mdbh	erb	abbarb	rich		gh_cer	gh_tot	logha	neardist	
age		**				*	**	**	*	
nalb		**	**			*	**	**		*
mdbh							**	**	*	
can				*				*		
erb										
lett					**	**				
abbarb				**				**		
narb					**	**		*		
rich						**				
shan										
gh_cer								*	**	*
gh_rov							**			
gh_tot										
volarb										
logha									**	**
par										
neardist										**
pch_buff720										
ha_buff720										
log_sem										
hdgxpch										
hdg_con										
pch_con										
ruscus										
crataegus										
cornus										
rosa										
rubus										
prunus										
ligustrum										
abbarb_sel										
ha_pch_con										
ha_buff497										
pch_buff497										

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Covariates correlations

	log_sem		hdg_con		ruscus		cornus		rubus		ligustrum		ha_pch_con		pch_buff497	
	ha_buff720	hdgxpch	pch_con	crataegus	rosa	prunus	abbarb_sel	ha_buff497	hdg_buff4							
age		*										*	*	*	*	**
nalb																
mdbh																
can						*										
erb						*										
lett				*		*										
abbarb				*	*	**	*	**	**		**	**				
narb				**	*	**	**	**	**		**	**				
rich				**	*	*		*	*							
shan				*	*	*		*	*							
gh_cer	*	*	*	*	*	*		*	*		*	*	*	*	*	*
gh_rov																
gh_tot								*	*		*	*	*	*	*	*
volarb		*		**	**	*	*	*	*	*	*	**	**	**	**	**
logha	**	**	**	**	**	*		*	*		**	**	*	*	*	*
par	*	*	**	*	*	*		*	*		**	**	**	**	*	*
neardist			**	*	*	*		*	*		**	**	**	**	*	*
pch_buff720	**	**	**	**	**	*		*	*		*	**	**	**	**	**
ha_buff720		**	**	**	**	*		*	*		*	**	**	**	**	**
log_sem			*	*	**	*		*	*		*	**	**	*	*	*
hdgxpch			**	**	*	*		*	*		**	**	**	**	**	**
hdg_con			**	**	**	*		*	*		**	**	**	**	**	**
pch_con				*	*	*		*	*		**	**	**	**	**	**
ruscus								*	*		*	**	**	*	*	*
crataegus									*		**	**	*	*	*	*
cornus									*		*	**	**	*	*	*
rosa									*		**	**	*	*	*	*
rubus									*		*	**	**	*	*	*
prunus									*		*	**	**	*	*	*
ligustrum									*		*	**	**	*	*	*
abbarb_sel									*		*	**	**	*	*	*
ha_pch_con									*		*	**	**	**	**	**
ha_buff497									*		*	**	**	**	**	**
pch_buff497									*		*	**	**	**	**	**

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

APPENDIX III

Table 1. Fragment fertilities of *M. avellanarius*. Number of offsprings in the litters found during the nest-boxes checks. Age class: 1 = absence of fur, offsprings weight lesser than 5 g; 2 = presence of fur, offsprings weight greater than 5 g.

Fragment	Litter size	Age class
MA1	4	1
MA2	1	2
MA3	2	2
MA3	2	2
MA6	2	1
MA8	3	1
MA8	6	2
MA8	4	1
MA8	5	1
MA8	3	1
MA8	6	1
MA8	7	1
MA8	5	2
MA8	3	2
MA8	2	2
MA9	3	2
MA9	2	2
MA9	2	1
MA9	2	2
MA9	4	2
MA9	2	2
MA9	2	1

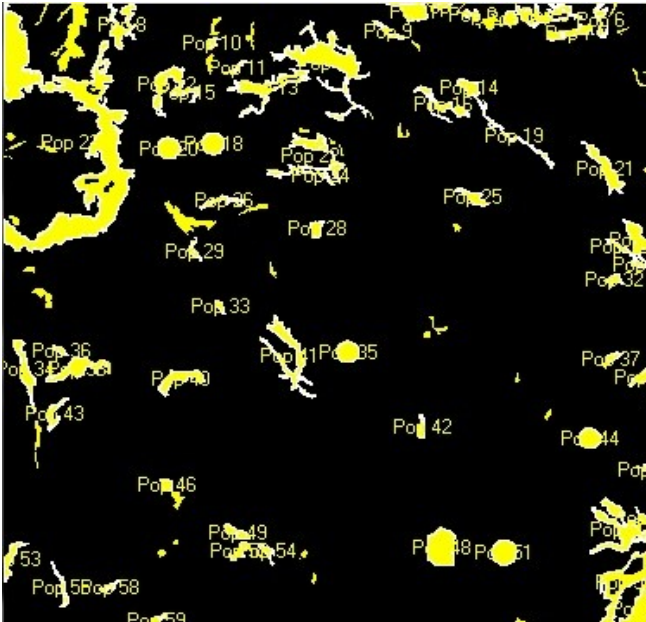
Table 2. Fragment fertilities of *M. glareolus*. Number of placental scars counted in the uteros on females died during the trapping sessions. Year: 1 = April 2011–February 2012; 2 = April 2012–February 2013.

Fragment	N. of placental scars	Year
MG12	4	1
MG12	4	1
MG12	2	1
MG12	3	1
MG12	5	1
MG12	0	1
MG12	4	1
MG12	0	2
MG12	3	2
MG12	3	2
MG12	0	2
MG20	3	1
MG20	4	1
MG20	4	2
MG20	4	2
MG20	3	2
MG20	7	2
MG20	5	2
MG2	4	1
MG2	4	1
MG2	4	2
MG2	3	2
MG2	4	2
MG2	4	2
MG2	4	2
MG2	4	2
MG21	3	1
MG21	6	1
MG21	3	1
MG21	5	1
MG21	4	2
MG21	4	2
MG14	7	1
MG14	2	1
MG14	6	2
MG23	5	1
MG23	3	1
MG9	0	2
MG9	4	2
MG9	5	2
MG9	6	2
MG13	3	2
MG17	2	2
MG17	1	2
MG17	1	2

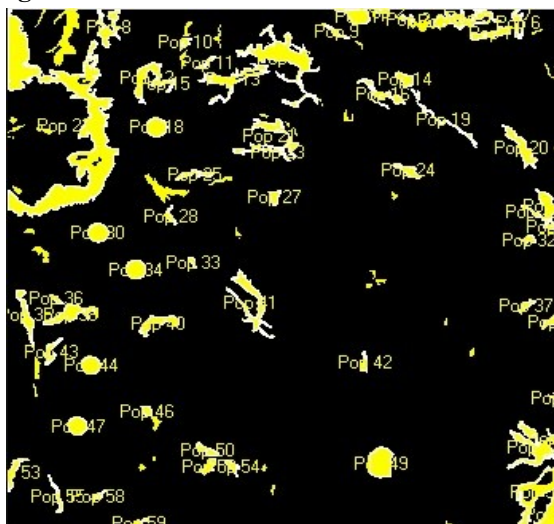
APPENDIX V

The following figures show the habitat suitability maps of the simulated landscape scenarios of the habitat restoration strategy on *M. avellanarius*.

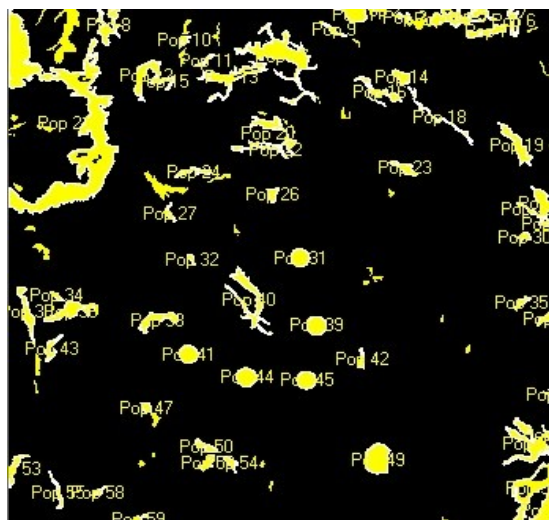
5 fragments of 10 hectares – 1



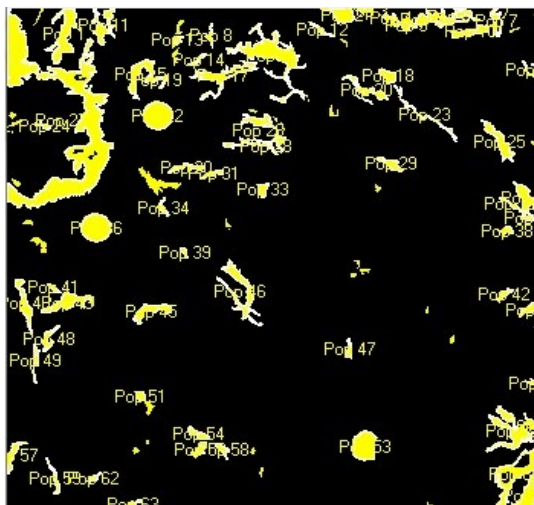
5 fragments of 10 hectares – 2



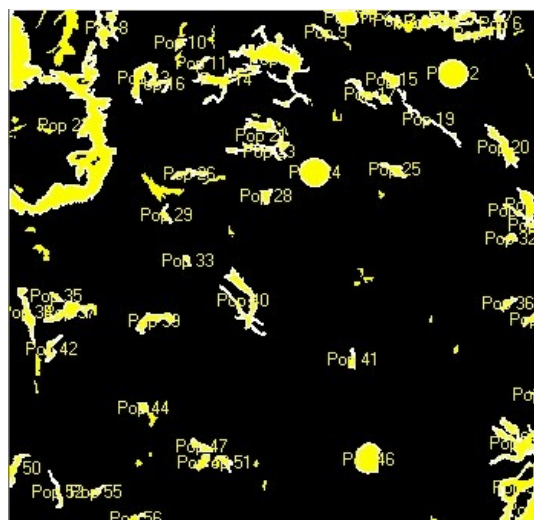
5 fragments of 10 hectares – 3



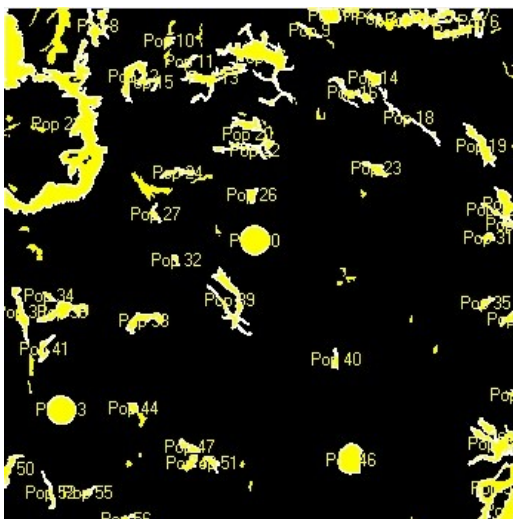
2 fragments of 25 hectares – 1



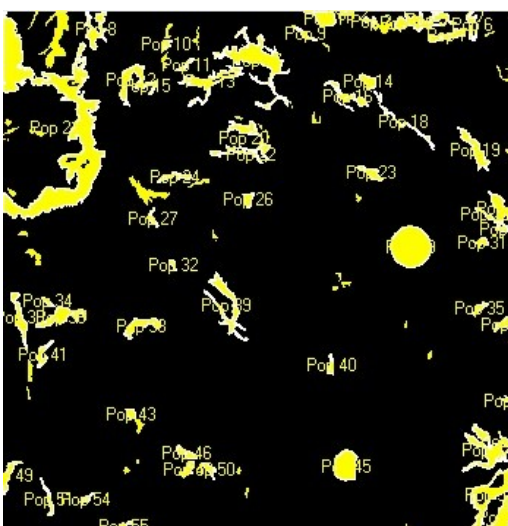
2 fragments of 25 hectares – 2



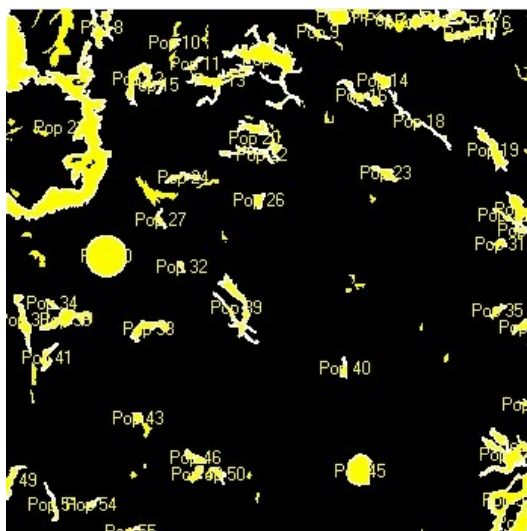
2 fragments of 25 hectares – 3



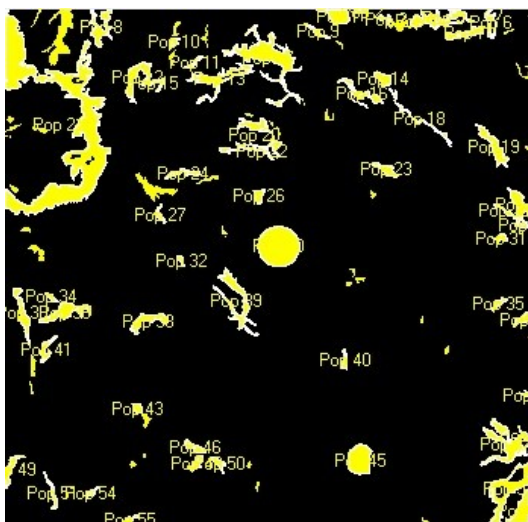
1 fragment of 50 hectares – 1



1 fragment of 50 hectares – 2



1 fragment of 50 hectares – 3



APPENDIX VI

Table 1. Monthly abundances of *Muscardinus avellanarius* in the investigated fragments.

Fragment	May10	Jun10	Jul10	Aug10	Sep10	Oct10	Nov10	May11	Jun11	Jul11	Aug11	Sep11
MA1	0	0	0	0	0	0	0	0	0	0	0	0
MA2	0	0	0	0	0	0	1	3	2	0	0	0
MA3	2	1	0	0	1	1	0	4	1	0	0	0
MA4	0	0	0	0	0	0	0	0	0	0	0	0
MA6	0	0	0	0	0	0	0	4	4	2	0	1
MA7	0	1	1	1	2	1	0	0	0	0	-	-
MA8	0	2	0	1	1	1	9	1	1	0	2	3
MA9	0	0	0	0	0	0	0	4	1	0	0	1

Fragment	Oct11	Nov11	Dic11	Apr12	May12	Jun12	Jul12	Aug12	Sep12	Oct12	Nov12	Dic12
MA1	0	0	0	0	1	4	1	0	0	0	0	0
MA2	0	0	1	1	3	1	0	0	0	2	1	3
MA3	1	7	7	0	0	0	0	0	0	0	0	0
MA4	0	0	0	0	0	0	0	0	0	1	0	0
MA6	1	0	1	0	0	0	0	0	0	0	0	0
MA7	-	-	-	-	-	-	-	-	-	-	-	-
MA8	1	7	4	6	4	0	3	0	1	0	0	0
MA9	0	8	16	4	4	0	2	4	3	0	0	0

Table 2. *Myodes glareolus* abundances observed during each trapping session in the investigated fragments.

Fragment	Apr 11	Jun 11	Aug 11	Oct 11	Dic 11	Feb 12	Apr 12	Jun 12	Aug 12	Oct 12	Dic 12	Feb 13
MG1	6	9	1	0	0	0	2	0	0	2	0	0
MG2	18	30	9	3	6	7	6	9	28	15	19	13
MG3	-	0	0	0	0	0	1	0	1	0	1	3
MG4	0	4	1	0	0	0	0	0	0	0	0	0
MG5	1	0	0	0	0	0	0	0	0	0	0	0
MG6	1	0	0	0	2	0	7	1	1	3	2	3
MG7	22	27	13	8	6	13	20	28	16	10	9	4
MG8	0	0	0	0	0	0	1	0	0	1	0	0
MG9	4	12	6	2	4	10	12	4	2	1	4	1
MG10	0	1	0	0	0	0	0	0	0	0	0	0
MG11	1	0	0	0	3	8	8	2	4	8	4	6
MG12	19	29	15	19	26	34	44	63	66	40	25	20
MG13	13	19	12	4	6	3	12	3	8	4	1	4
MG14	6	4	3	1	1	5	9	5	10	6	4	3
MG15	10	9	2	2	3	0	4	0	2	0	1	1
MG16	3	3	2	1	2	5	11	6	2	1	0	0
MG17	2	7	2	2	2	4	6	1	8	5	1	6
MG18	0	6	2	0	2	8	13	1	1	0	1	5
MG19	2	0	0	0	0	0	1	0	4	2	1	7
MG20	0	15	12	3	6	22	26	11	16	18	9	7
MG21	-	30	21	15	9	24	13	6	13	20	19	14
MG22	0	2	0	0	0	0	0	0	0	0	0	0
MG23	1	2	0	1	1	2	7	1	7	0	4	10
MG24	2	4	0	0	1	2	1	0	0	0	0	1
MG27	0	10	4	1	3	7	11	12	9	-	-	0
MG28	-	2	1	0	0	0	3	2	2	2	2	1
MG29	3	3	1	0	0	1	6	3	5	6	5	3